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Vol. 71 JANUARY, 1944 No. 1

Bulletin

of the

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Published for the Club bi-monthly
by
THE SCIENCE PRESS PRINTING COMPANY
N. QUEEN ST. AND McGOVERN AVE.
LANCASTER, PENNSYLVANIA

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The Bulletin of the Torrey Botanical Club

Subscriptions, dues, and inquiries about back numbers should be sent to the office of publication, N. Queen St. and McGovern Ave., Lancaster, Pa., or to Page J. Karling, Department of Botany, Columbia University, New York 27, N. Y. Correspondence about advertisements and circulation should be addressed to Dr. Harold H. Clum, Hunter College, New York 21, N. Y. Communications about exchanges should be sent to Dr. Edwin B. Matzke, Department of Botany, Columbia University, New York 27, N. Y. Manuscripts intended for the Bulletin should be sent to Dr. H. W. Rickett, The New York Botanical Garden, New York 58, N. Y.

Claims for missing numbers must be made within 60 days from the date of issue.

The subscription price of the Bulletin of the Torrey Botanical Club is $6.00 a year except to active members of the Club. Of the annual membership dues, $3.00 covers a year's subscription to the Bulletin.

Torreya. Bimonthly; established 1901. Of the annual dues $0.50 is for a year's subscription to Torreya; price to non-members, $1.00.

Entered as second-class matter October 8, 1940 at the post office at Lancaster, Pa., under the Act of March 3, 1879. Accepted for mailing at the special rate of postage provided for in the Act of February 28, 1925, embodied in paragraph 4, section 538, P. L. & R.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 71, No. 1, pp. 1–10 JANUARY, 1944

TEMPERATURE, THIAMINE, AND GROWTH OF PHYCOMYCES

WILLIAM J. ROBBINS AND FREDERICK KAVANAGH

Temperature has a marked effect upon the growth of *Phycomyces blakesleeanus* in media containing limiting amounts of thiamine. At the lower temperatures growth is slower but the sporangiophores attain a greater length and the final dry weight of the mycelium is materially larger. The interrelation between thiamine and temperature on the growth of *Phycomyces* may affect our ideas of the metabolism of thiamine by this organism, bears on the use of this fungus in the bioassay of thiamine, and modifies our concept of the term "optimum" temperature. The present study reports experiments on the growth of *Phycomyces* in solution cultures at various temperatures in the presence of limiting amounts of thiamine or its intermediates.

METHODS AND MATERIALS

Phycomyces blakesleeanus (+) was grown in 125-ml. Erlenmeyer flasks each containing 25 ml. of a basal medium[1] supplemented with thiamine (or mixtures of its intermediates) in amounts less than sufficient to allow maximum growth. The medium in the flasks was inoculated by adding a drop of a spore suspension in sterile distilled water. Identical cultures were incubated at various temperatures; at intervals after inoculation the dry weights of the mycelium were determined. The dry weights of small quantities of mycelium were determined by filtering into Gooch crucibles, washing thoroughly with distilled water, and drying at 100° C. When growth was sufficiently extensive to form a mat, the mat was fished out, washed in distilled water, pressed partially dry with the fingers and placed in aluminum pans for drying and weighing.

All glassware was cleaned with chromic acid cleaning mixture, thoroughly rinsed with tap and distilled water, and drained dry. The thiamine and its intermediates were obtained from Merck and Co. The asparagine was purified by treatment with Norit and crystallization from alcohol. The other chemicals were of C.P. grade.

EXPERIMENTS

Dry Weight—Time Curves at Various Temperatures. *Phycomyces* was grown at 10°, 15°, 20°, and 25°[2] in the basal medium with 3 g. of

[1] The basal solution contained per liter 0.5 g. $MgSO_4 \cdot 7H_2O$, 1.5 g. KH_2PO_4, 50 g. dextrose, asparagine as indicated, and the following trace elements in p.p.m.: 0.005 B, 0.02 Cu, 0.1 Fe, 0.01 Mn, 0.01 Mo, 0.09 Zn, and 0.01 Ga.

[2] For simplicity the temperatures of incubation are given to the nearest whole degree. They were actually as follows: 10.4° ± 0.2, 15.4° ± 0.4, 20.0° ± 0.3, and 24.8° ± 0.3. All temperatures are expressed on the Centigrade scale.

asparagine per liter supplemented with 0.25, 0.5, 1.0, or 1.5 mμ moles of thiamine per flask. At various intervals after inoculation the dry weights[3] of triplicate cultures were determined.

The most complete series of determinations was made on those cultures supplemented with 1.0 mμ mole of thiamine. For the cultures grown with this

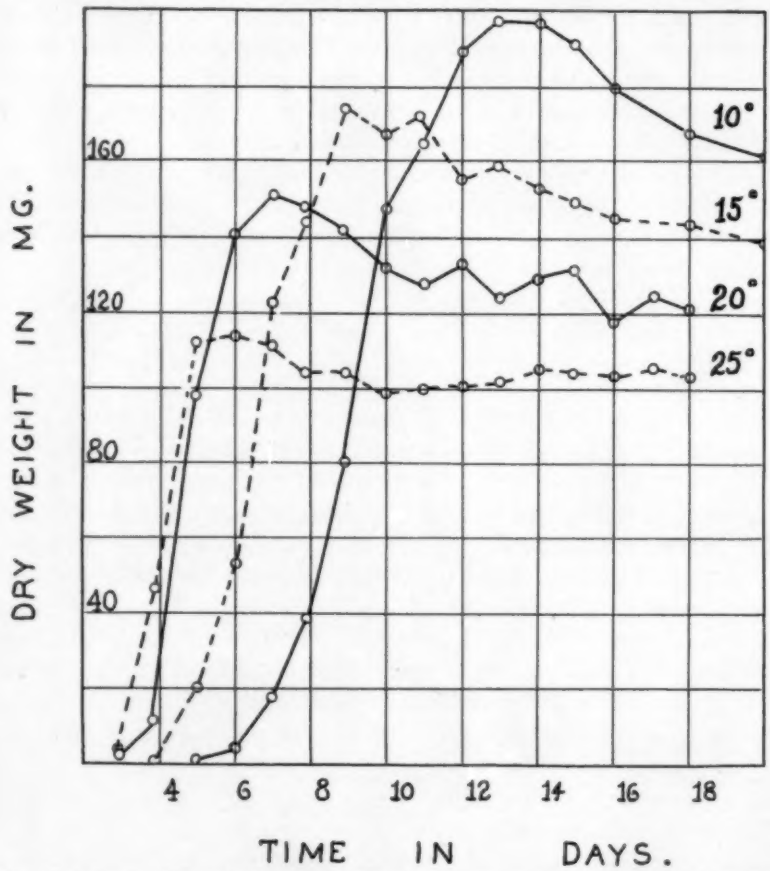

FIG. 1. Average dry weights of mycelium of *Phycomyces* produced at 10°, 15°, 20°, and 25° in a basal solution containing 1 mμ mole thiamine per flask.

amount of thiamine at 10° dry weights were determined daily from the 5th to the 16th day after inoculation and on the 20th, 22nd, 24th, and 26th day. For those cultures at 15° dry weight determinations were made daily from the 4th to the 16th day and on the 18th, 20th, and 22nd day. For the cultures

[3] In this experiment variations in water content in the dried mycelium were minimized by removing the mycelium from the oven and allowing it to cool for at least 30 minutes in a desiccator over calcium chloride. Weighings were made to the nearest 0.1 mg. in 30 seconds.

at 20° and 25° the determinations were made daily from the 3rd to the 18th day. The dry weight—time curves (fig. 1) at all four temperatures were of the same general shape. At each temperature the dry weight increased with time to a maximum followed by a decrease as the result of autolysis. The higher the temperature the more quickly the maximum was reached and the lower was that dry weight. At 10° with 1.0 mμ mole of thiamine the maximum dry weight was 196.8 mg. reached on the 13th day; at 15°, 167.9 mg. on the 10th day; at 20°, 152.9 mg. on the 7th day, and at 25°, 113.6 mg. on the 6th day. Almost twice as much dry matter was produced by *Phycomyces* at 10° with 1.0 mμ mole of thiamine as was formed in the same medium at 25°.

TABLE 1. *Average dry weight in mg. of mycelium of Phycomyces grown at 10°, 15°, 20°, or 25° for the periods given in a basal solution containing 0.25, 0.5, 1.0, or 1.5 mμ moles of thiamine*

Days:		5	7	10	12	13	18	20	22	28
0.25 mμ mole thiamine	10°	.....	21.7	58.0	72.9	.....	.....	54.1	.....	52.2
	15°	18.7	51.8	62.6	.....	53.1	.....	.....	51.0	.....
	20°	47.6	51.2	41.6	.....	43.8	51.3	.....	.....	.....
	25°	42.5	38.4	38.6	.....	39.6	43.5	.....	.....	.....
0.5 mμ mole thiamine	10°	.....	24.5	105.1	129.5	.....	.....	101.0	.....	90.7
	15°	28.2	95.6	105.5	.....	89.6	.....	.....	84.3	.....
	20°	85.8	86.3	71.0	.....	68.0	67.2	.....	.....	.....
	25°	71.2	70.1	66.9	.....	63.7	66.1	.....	.....	.....
1.0 mμ mole thiamine	10°	2.0	18.3	148.3	189.8	196.8	168.3	162.2	151.5	135.9
	15°	20.2	123.1	167.9	157.8	159.1	143.4	139.9	133.3	.....
	20°	99.2	152.9	132.4	133.2	124.5	122.0	.....	.....	.....
	25°	113.3	112.3	99.2	101.1	102.9	104.1	.....	.....	.....
1.5 mμ moles thiamine	10°	.....	46.5	203.4	225.8	.....	.....	180.8	.....	160.5
	15°	58.6	187.5	190.0	.....	181.7	.....	.....	161.2	.....
	20°	179.0	186.8	186.5	.....	167.8	161.5	.....	.....	.....
	25°	156.4	153.7	133.2	.....	133.5	141.7	.....	.....	.....

Less frequent determinations of dry weights were made with the other quantities of thiamine. At 10° determinations were made on the 7th, 10th, 12th, 20th, and 26th day; at 15°, on the 5th, 7th, 10th, 13th, and 22nd day; at 20° and 25°, on the 5th, 7th, 10th, 13th, and 18th day. The results (table 1) with 0.25, 0.5, or 1.5 mμ moles of thiamine per flask were similar to those obtained in the cultures which contained 1.0 mμ mole of vitamin. The maximum dry weight attained at the lower temperatures was greater than that at the higher temperatures (table 2). In the cultures containing 0.25 mμ mole of thiamine the maximum weight at 10° was 171 per cent of the maximum at 25°; in those with 0.5 mμ mole it was 182 per cent; with 1.0 mμ mole 174 per cent; and with 1.5 mμ moles 155 per cent.

The higher the temperature the less efficiently was thiamine used by *Phycomyces* in the production of dry matter. This is made clear by the

figures in table 2 and also by calculating the dry matter formed per unit of thiamine at the various temperatures. For example, in the presence of 1 mμ mole of thiamine *Phycomyces* at 10° produced 580,000 units of dry matter for each unit of thiamine present in the medium; at 25° the units of dry matter per unit of thiamine were 340,000.

It should be emphasized that the amount of thiamine in these cultures was the factor limiting growth at all temperatures. More than sufficient sugar, asparagine, mineral salts, and other materials were present for the amount of growth obtained. This is demonstrated by the increased growth as the thiamine was increased. For example, the maximum at 10° with 0.25 mμ mole of thiamine was 72.9 mg.; with 0.5 mμ mole, 129.5 mg.; with 1.0 mμ mole, 196.8 mg.; with 1.5 mμ moles, 225.8 mg. Similar results were obtained at 15°, 20°, and 25° (table 2).

TABLE 2. *Maximum dry weights in mg. obtained at the temperatures and with the quantities of thiamine given. The figures in the parentheses are the number of days of incubation to obtain the maximum dry weight.*

Mμ moles thiamine	10°	15°	20°	25°
0.25	72.9 (12)	62.6 (10)	51.3 (7)	42.5 (5)
0.5	129.5 (12)	105.5 (10)	86.3 (7)	71.2 (5)
1.0	196.8 (13)	167.9 (10)	152.9 (7)	113.3 (6)
1.5	225.8 (12)	190.0 (10)	186.8 (7)	156.4 (5)

Two grams of asparagine per liter were found to be insufficient to allow maximum growth at 10° C in the presence of 1 mμ mole of thiamine though entirely adequate when 0.2 mμ mole of thiamine was used.

The Influence of Excess Thiazole or Pyrimidine on the Efficiency of Thiamine at Various Temperatures. Bonner and Buchman (1) pointed out that the dry matter produced by *Phycomyces* in the presence of a limiting amount of thiamine was materially increased if an excess of the thiazole intermediate of thiamine was present. This "thiazole effect" on *Phycomyces* was confirmed by Robbins and Kavanagh (4) and by Kavanagh (3). It appeared desirable to determine the influence of temperature on the thiazole effect.

Phycomyces was grown in the basal medium containing 4 g. of asparagine per liter supplemented per culture with mixtures of the pyrimidine and thiazole[4] intermediates of thiamine as follows:

0.25 mμ mole pyrimidine and 0.25 mμ mole thiazole
0.25 mμ mole pyrimidine and 10.0 mμ moles thiazole
10.0 mμ moles pyrimidine and 0.25 mμ mole thiazole

[4] The thiazole used was 4-methyl-5-β-hydroxyethylthiazole and the pyrimidine was 2-methyl-5-bromomethyl-6-aminopyrimidine hydrobromide.

1.0 mμ mole pyrimidine and 1.0 mμ mole thiazole
1.0 mμ mole pyrimidine and 10.0 mμ moles thiazole
10.0 mμ moles pyrimidine and 1.0 mμ mole thiazole

Dry weights were determined on duplicate cultures at 25° after 4, 5, 6, 7, 9, and 11 days of incubation, and at 10° after 9, 11, 12, 13, 15, and 26 days. These days were selected because it was anticipated from the earlier results with thiamine that they would probably cover the maximum growth period.

In the cultures with equimolecular amounts of thiazole and pyrimidine the results were much like these obtained in the earlier experiment with thiamine. At 10° the maximum growth obtained with 1 mμ mole of thiamine was 196.8 mg. (table 2), and with 1 mμ mole of each of the two intermediates it was 192.9 mg. (table 3). At 25° the maximum growth with 1.0 mμ mole of

TABLE 3. *Dry weights in mg. of the mycelium of Phycomyces grown for the periods given in mixtures of the pyrimidine (Pyr.) and thiazole (Th.) intermediates of thiamine. Above, temperature of incubation 25°; below, temperature of incubation 10°.*

Days	0.25 mμ mole Pyr. 0.25 mμ mole Th.	0.25 mμ mole Pyr. 10.0 mμ moles Th.	10.0 mμ moles Pyr. 0.25 mμ mole Th.	1.0 mμ mole Pyr. 1.0 mμ mole Th.	1.0 mμ mole Pyr. 10.0 mμ moles Th.	10.0 mμ moles Pyr. 1.0 mμ mole Th.
4	22.7	19.5	23.0	16.7	33.1	15.0
5	43.3	26.4	46.8	90.5	123.7	112.8
6	42.6	61.2	48.3	108.8	152.8	116.7
7	38.8	64.5	43.3	104.0	169.4	118.1
9	37.2	63.8	42.1	95.7	172.3	110 5
11	36.8	60.5	39.5	90.0	180.1	107.5
9	38.7	38.7	27.8	41.2	43.1	39.1
11	55.9	62.5	56.7	157.2	148.4	162.3
12	62.8	67.3	63.5	190.1	207.0	191.7
13	64.8	63.8	65.5	192.9	215.9	198.5
15	58.9	74.5	64.1	191.2	210.5	203.3
26	54.7	80.1	57.3	172.6	196.1	170.1

thiamine was 113.3 mg., and with 1 mμ mole of each of the two intermediates 108.8 mg. At 10° the maximum yield with 0.25 mμ mole of thiamine was 72.9 mg., and with 0.25 mμ mole of the intermediates 64.8 mg.; at 25° 0.25 mμ mole of thiamine gave 42.5 mg. as the maximum dry weight while 0.25 mμ mole of the two intermediates produced 43.3 mg. The maximum growth at 10° was 179 per cent greater than at 25° in the cultures with 1 mμ mole of each of the two intermediates, and 150 per cent greater in the cultures with 0.25 mμ mole of the intermediates.

The thiazole effect was evidenced at both temperatures but it was more pronounced at 25° than at 10°. In the cultures at 25° supplemented with 1 mμ mole of pyrimidine and 10 mμ moles of thiazole the maximum dry weight was 180.1 mg. as compared to 108.8 mg. where equimolecular amounts

of the two intermediates were used (table 3). At 10°, however, the maximum yield with 1 mμ mole of pyrimidine and 10 mμ moles of thiazole was 215.9 mg. as compared to 192.9 mg. in the solutions containing 1 mμ mole of each of the intermediates. The maximum dry weight at 25° in the solutions containing excess thiazole was 173 per cent of that in the solutions containing

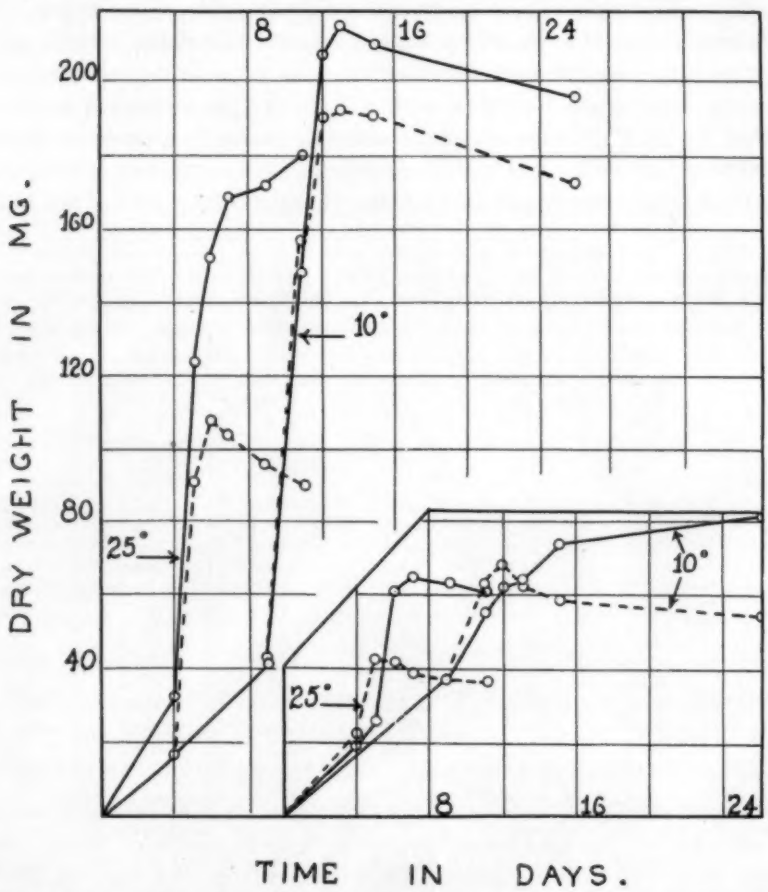

FIG. 2. Average dry weights of mycelium of *Phycomyces* produced at 10° and at 25° in solutions containing equimolecular quantities of the thiazole and pyrimidine intermediates and in solutions with excess thiazole. Above, solutions containing per flask 1 mμ mole each intermediate (broken line), or 1 mμ mole pyrimidine and 10 mμ moles thiazole (solid line). Below, solutions containing 0.25 mμ mole of each intermediate (broken line), or 0.25 mμ mole pyrimidine and 10 mμ moles thiazole (solid line).

equimolecular amounts of the two intermediates; at 10°, however, it was 112 per cent. In fact, the growth at 25° in the cultures supplemented with excess thiazole approached that at 10° in the cultures containing 1 mμ mole of each of the intermediates (fig. 2).

The same sort of results was obtained with the smaller amounts of the intermediates. The maximum dry weight at 25° in the cultures with 0.25 mμ mole of each intermediate was 38.8 mg. and with 0.25 mμ mole of pyrimidine and 10 mμ moles of thiazole it was 150 per cent greater (64.5 mg.). On the 13th day at 10° the dry weights in the solutions with equimolecular amounts of the two intermediates nearly equaled that in the solutions with excess thiazole. In the latter solutions, however, the dry weight continued to increase, reaching a value (80.1 mg.) 120 per cent greater than the maximum found in the solution with equimolecular amounts of the intermediate.

A lower temperature of incubation had much the same effect on the dry weight of *Phycomyces* under our conditions as the addition of excess thiazole to the medium. For example, the maximum dry weight at 10° with 0.25 mμ mole of the intermediates was 64.8 mg., and it was 64.5 mg. at 25° when the solution contained 0.25 mμ mole of pyrimidine and 10.0 mμ moles of thiazole. The maximum dry weight at 10° in the solutions with 1 mμ mole of the intermediates was 192.9 mg., and at 25° in the solutions containing 1 mμ mole of pyrimidine and 10 mμ moles of thiazole it was 180.1 mg. In fact, the weight (90.0 mg.) with 1 mμ mole of the intermediates at the end of 11 days growth at 25° was nearly the same as that (80.1 mg.) obtained with 0.25 mμ mole of pyrimidine and 10 mμ moles of thiazole at the end of 26 days at 10°.

Excess pyrimidine had little effect on the dry weight of *Phycomyces* as compared to that in the solutions containing equimolecular amounts of the two intermediates (table 3). There was a slight though consistently greater dry weight in those solutions containing excess pyrimidine, but whether this was a real effect or the result of some systematic error is uncertain. In any event, the action of excess pyrimidine was in no way comparable to that of excess thiazole.

DISCUSSION

Optimum Temperature for Dry Matter Production by Phycomyces. Burkholder and McVeigh (2) grew *Phycomyces* at 10°, 15°, 20°, and 25° with various amounts of thiamine, and concluded that the optimum temperature for the production of dry matter lies in the vicinity of 15° under the conditions of their experiments. However, they neglected the time factor and determined dry weights at one point only, namely, at the end of 10 days, a length of time insufficient for the cultures at 10° to attain their maximum dry weights. Our data show that the optimum temperature for the production of dry matter by *Phycomyces* in the presence of limiting amounts of thiamine is 10° or less. In fact, extrapolation of our data suggest that if *Phycomyces* could be grown at so low a temperature, the maximum dry weight at 2° with 1 mμ mole of thiamine per flask and 4 g. of asparagine per liter would be about 250 mg. and the thiazole effect would not appear.

The optimum temperature for the production of dry matter is influenced by the composition of the medium. We were concerned with the effects of temperature when the supply of thiamine was the limiting factor for growth. Different results would have been obtained if asparagine, dextrose, or some factor other than thiamine were limiting. For example, when 2 g. of asparagine per liter were used, we found the difference in maximum dry weights at 10° and 25° in the presence of 1 mμ mole of thiamine to be small, 126.5 mg. at the lower temperature as compared to 117.6 mg. at 25°. When 3 g. of asparagine per liter were furnished these weights were 197.2 mg. and 115.2 mg. respectively.

With the smaller amounts of thiamine Burkholder and McVeigh (2) found maximum growth at 15° C, but when 12.5, 25.0, or 2500.0 mμ moles of thiamine were supplied per flask the dry weights at the end of 10 days were nearly the same at 15°, 20°, and 25° C. They concluded that the extension of the optimum temperature range with the larger amounts of thiamine was related to the heterotrophic requirement of the fungus for thiamine. It is more probable that this apparent extension of the optimum temperature range was because asparagine or glucose limited growth in those cultures which were supplied with relatively large amounts of thiamine.

Significance for the Bioassay of Thiamine. It is clear that the temperature of incubation is important in the assay of thiamine by the growth of *Phycomyces*. A standard curve showing the relation between amount of thiamine and growth of *Phycomyces* at one temperature cannot be satisfactorily used for the bioassay of thiamine at another temperature. For example, 100 mg. of dry matter on a standard curve constructed from our data showing the relation between quantity of thiamine and maximum dry weight (5 days growth) of *Phycomyces* at 25° would represent the effect of 0.84 mμ mole of thiamine (fig. 3). If, however, the fungus were grown at 15° when a bioassay was made, a maximum dry weight of 100 mg. (10 days growth) would be produced with 0.47 mμ mole of thiamine (fig. 3). An error of comparable magnitude results if the dry weights obtained from older cultures are used instead of those which are maxima. A dry weight of 100 mg. with 10-days-old mycelium grown at 25° represented 0.98 mμ mole of thiamine as shown by our data. But 100 mg. of mycelium were produced in 20 days at 15° by 0.62 mμ mole of thiamine (fig. 3).

Relation to Concepts of the Metabolism of Thiamine. Are the results obtained with *Phycomyces* applicable to other organisms? For example, to those which require molecular thiamine and are unable to utilize the intermediates?

Bonner and Buchman (1) were of the opinion that *Phytophthora cinnamomi*, which is unable to use the intermediates of thiamine, destroys thia-

mine in the same way that *Phycomyces* does. This, they believe, occurs by the inactivation of the thiazole portion of the thiamine molecule and the releasing of functional pyrimidine. *Phycomyces* is able to couple the residual

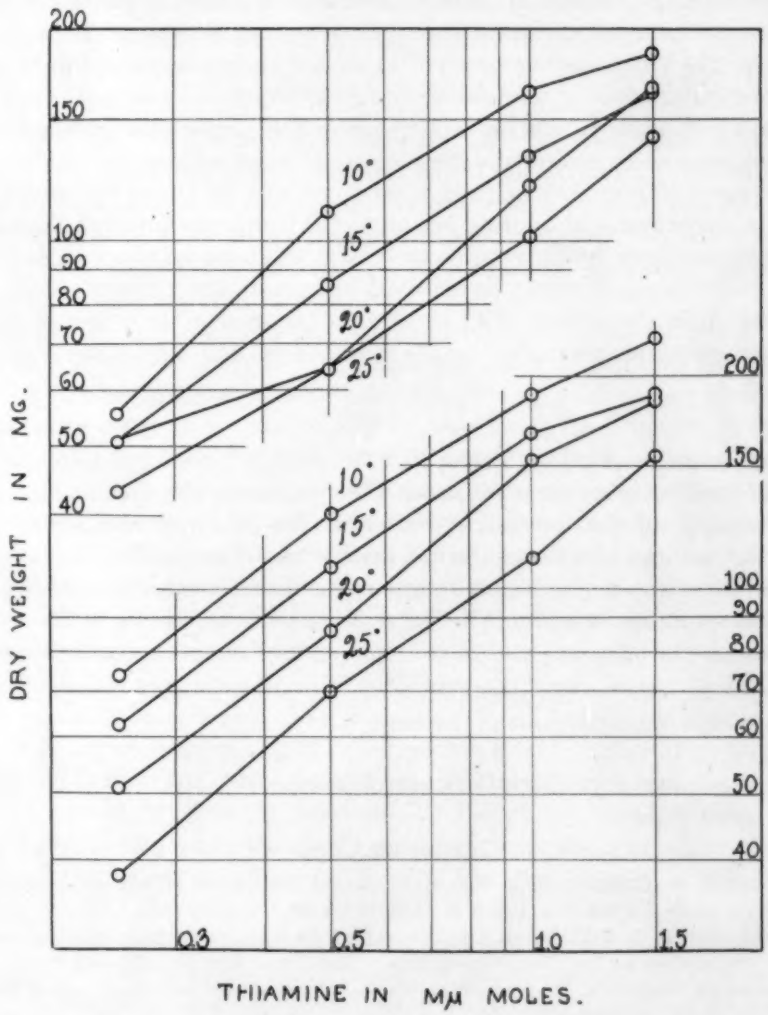

FIG. 3. Dry weights of *Phycomyces* at various temperatures plotted against quantity of thiamine on log log scales. Lower curves maximum weights at various temperatures used. Upper scale weights after 22 days at 10°; after 20 days at 15°; after 18 days at 20° and 25°.

pyrimidine with additional thiazole to form thiamine. *Phytophthora* cannot do this.

If Bonner and Buchman are correct then we should expect organisms requiring molecular thiamine also to utilize thiamine more efficiently at the lower temperatures than at higher temperatures.[5]

Kavanagh (3), however, has suggested that two enzyme systems in *Phycomyces* compete for thiamine, carboxylase and an enzyme which destroys thiazole. The latter enzyme does not exist in *Phytophthora*. If this is true, then the major effect of temperature on *Phycomyces* may be on the enzyme system which destroys thiazole rather than on the carboxylase system. Under such circumstances a marked difference might exist between the response to temperature of *Phycomyces* (and other fungi able to utilize the intermediates) in the presence of limiting amounts of thiamine, and that of organisms like *Phytophthora* which require molecular thiamine. A decision between these two viewpoints might be obtained by investigating the effect of temperature upon the growth of *Phytophthora* (or some other organism which requires molecular thiamine) in the presence of limiting amounts of this vitamin.

SUMMARY

Phycomyces was grown at 10°, 15°, 20°, and 25° in a basal solution containing limiting amounts of thiamine. The maximum dry weight increased as the temperature of incubation decreased. The efficiency with which thiamine was used by this fungus in the production of dry matter was greater at the lower than at the higher temperature. The benefit of excess thiazole was greater at 25° than at 10°. The relation of these results to the use of *Phycomyces* in bioassays and to concepts of the metabolism of thiamine is discussed.

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[5] This conclusion would not necessarily follow if the effect of temperature on *Phycomyces* described here resulted solely from the influence of temperature upon the recombination of thiazole and pyrimidine since *Phytophthora* is incapable of this synthesis.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 71, NO. 1, PP. 11–22 JANUARY, 1944

POLLEN ANALYSIS OF SOME BURIED SOILS, SPARTANBURG COUNTY, SOUTH CAROLINA[1]

STANLEY A. CAIN

In 1936 the Soil Conservation Service[2] made a reconnaissance of the southern Piedmont and selected Spartanburg County, South Carolina, as a locale for intensive study of natural and accelerated erosion from the geological point of view. This is an area in which gullying has been particularly destructive because of the nature of the coincidence of land form, land use, soils, deep weathering, and climate.

The Piedmont topography of Spartanburg County is of the gently rolling type that results from the long-continued action of running water. The rounded divides slope gradually into dale heads, shallow saucer-shaped slopes, which everywhere connect with the ravines of the dendritic drainage pattern. The greater part of the area is underlaid by granites, gneisses, and schists, which under the warm, humid climate have generally weathered from 25 to 50 feet, and on the interstream divides to twice that depth below the surface. The residual soils of the area (Cecil, Lockhart, Appling, Colfax, etc.) are intimately related to the bedrock, with a badly decomposed layer, which retains the original rock structure and arrangement, intermediate between bedrock and soil.

Not only are the gullies from 20 to 25 and sometimes 50 feet deep, but a single rain may cause a gully to widen from 10 to 12 feet in places, and its cave head may recede from 10 to 15 feet within a few months. If it were not for erosion of this type, which takes place principally away from the permanent streams of the area, in dales and on the upper slopes of the gentle topography, no one would have had reason to suspect the presence of numerous, local, buried, organic soils.

Late in 1938 the author was invited to inspect certain of these organic horizons which had been discovered as a result of the gully studies around Spartanburg, and to apply the technique of pollen analysis to them, should their characteristics seem to warrant doing so. In every case these sediments, at the heads of rapidly growing gullies, rest near the upper surface of the saprolite, separated from it only by a thin sand and gravel bed, and are

[1] Contribution from the Botanical Laboratory of The University of Tennessee, N. S. No. 70.

[2] The following introductory paragraphs are based upon a publication of the S.C.S., "Principles of Gully Erosion in the Piedmont of South Carolina" by H. A. Ireland, C. F. S. Sharpe, and D. H. Eargle. U. S. Dept. Agr. Tech. Bull. 633. 1939. The author wishes to thank Mr. Eargle for invaluable field assistance.

buried from 5 to 20 feet or more under inorganic soils which have the typical profile structure of the residual soils of the area. After a preliminary reconnaissance and laboratory examination of some samples of these buried soils —which frequently yielded an abundance of pollen grains and spores—it was decided to study systematically some of the exposed sections with a view to seeking a possible answer to some questions with which the Division of Physiographic and Climatic Research of the Soil Conservation Service was concerned: namely, are the buried organic soils of geological age, or was their burial historic and a result of accelerated erosion following agriculture? Was the vegetation of the vicinity during the period of sedimentation similar to that prevailing today, or was it of a type associated with an entirely different climatic regimen?

METHODS

Materials for the study of several complete sections were obtained, and the present report is concerned with four apparently typical profiles from gullies here referred to as stations I (Mt. Collins, South); II (Mt. Collins, North); IV (Fingerville); and VIII (Pauline). At each station the profile, exposed in the vertical wall or head of the gully, was sampled by removal from the cleaned surface of blocks of peaty or organic soil measuring $1 \times 1 \times 1.5$ inches. The samples were numbered from the base of the sedimentary layer upward and were taken at 3-inch intervals, i.e., with an unsampled 2-inch section between each sample. The samples were cleaned by trimming the surfaces and each sample was placed in a separate pill box where it was allowed to dry.

In the laboratory the dry, hardened samples were again cleaned by trimming, and material for the preparation of slides was shaved from the surfaces and gently powdered. The powder was passed through a brass sieve and collected in a centrifuge tube by means of a funnel. The material of a sample remained in its tube throughout the steps of preparation by the Erdtman acetolysis method (Cain 1939, p. 633). After the last centrifuging of the material all the alcohol was decanted except for about 0.5 cc., which was gently agitated in order to produce a suspension of the pollen-bearing material of the surface of the precipitate. Enough of this suspension was mounted in Sirtillac to make about 20 sq. cm. of prepared slide surface. Safranin was used as a stain, and in most preparations the pollen grains and spores were in good condition and readily studied.

The slides were examined under a binocular at a magnification of 440 diameters. A mechanical stage was employed, and strips across a slide the width of the field of vision were examined completely. For each sample enough slide area was studied to yield a minimum of 150 pollen grains of dominant tree species. All other identifiable objects were also recorded while these grains were being sought.

TABLE 1

Sample number	Woody plants: Dominant trees: Conifers: Pinus	Picea	Abies	Fragments	Oak-Hickory: Quercus	Carya	Castanea	Mesophytes: Tsuga	Betula	Carpinus	Liquidambar	Tilia	Nyssa	Fagus	Edaphic trees + shrubs: Alnus	Salix	Ericaceae	Non-woody plants: Flowering plant families: Gramineae	Cyperaceae	Compositae	Onagraceae	Nymphaeaceae	Amaranthaceae	Spores: Asplenium	Sphagnum	Osmunda	Lycopodium	Miscellaneous	Undetermined	Undeterminable	Total
Station I Mt. Collins South																														
10	127			35	2		2		1						10	8			20	5			1	6	60	1		4	7	7	298
9	140	3		26	5			1							7	2		1	74	1		1		1	5	3			1	7	278
6	148	4	2	65	27	3	3	3	2	1					9	2	11	18	3	26		5	1	72	37			1	6	3	9	457
5	126	23	4	80	45	4	14	3	7						17	2	3	101	6	47		8	1	37	25					6	43	602
4	66	3	6	31	41	17	9	15	5	1					37	13	13	37	12	54	2	3		34	25				13	12	19	468
3	114	17	1	20	12	1	15		1						13	4		41	12	8		1	2	4	5					11	24	306
1	36	5		36	2		1								4					1				2	1		1				89
Station II Mt. Collins North																														
12	32			58	73	4	41		9		1				81	11	3	17		45			2	4	7					9	397
11	58			64	82	8	7		24	2	1				5	5	6	2	7	35			5	4	2			3	4	16	340
10	57			79	56	1	27	3	14						25	12	7	4		26	2	1	4	5	3				1	23	350
9	66	7	3	92	46	4	21		25						17	7	26	16	5	24	2	1	3	23	17				3	5	413
8	8			36	68	5	21		44	20	1				60	11	7	12	10	21			9	5	26	2			7	8	381
6	94		9	110	30	3	3		9	1	1				10	8	6	20	6	15	2		9	12	14		1		1	26	390
5	5			22	82	1	53		14	13					112	39	10	42		75			64	2	21	8			2	20	585
3	83		3	97	33	18	12	4	6	1		1			8	14	3	1	3	23	3	1		30	2			2	3	8	360
2	34			24	85	23	19		13	8		1			31	13	10	7	4	59		3		14	10		1	1	3	26	391
Station IV Fingerville																														
10	20	2		43	66	46	14		4		2		2		90	5		6	5	43			11	14			10	2	5	15	405
9	61	3		65	54	8	21	4	6						119	3	2		12	14			8	6			1		1	9	397
8	62			77	59	24	2	5						2	21	4	1		3	10				32			3	3	1	11	320
7	97			47	37	21	3	1		1	2	2			64	5	1	3	7	8			10	21	2		2		2	9	345
6	61		9	66	53	21		4	2		4			2	24	4	1			5		1	1	22			4	4		16	304
5	71	11	24	68	37	12		10			2				15	1	1			4				31				1		8	296
4	86	3	20	64	25	17		9			1				32	1	1			4				25			1	1		8	298
3	100		9	79	19	17		8	3		1			2	27	3			3	4				13			1	1	2	3	295
2	63		17	96	33	27	4	15	4		1			6	7		1						1	27	2		3		1	2	310
1	68	4	18	76	22	23	6	18			1		4		1		1		2	2				22	1		1	1	1	7	279
Station VIII Pauline																														
23	11			31	107	12	10							1	12	3	3			21				2					2	2	215
22	21	6	2	69	36	29	9										1			6				6						5	190
20	5			17	123	15	44							2	3	2				4										4	219
19	8			10	130	10	18						1	1	4		2			4				9					1	3	201
18	5			26	132	8					2		3				1			5			8	8				3	2	6	209
17	19			39	112	17	4								1		6			1				3						3	205
16	9			8	126	23	12							2	3	1	2			3				3						3	195
15	15			10	95	20	51								8		1	2		4				5						3	214
13	14			30	138	39	48								4					9			4	5						5	306
11	4	1		7	116	7	21		6		5				43	6		21		12			4	5				1		9	269
10				8	82	6	86		3						57	1		9		27			7	9						6	300
9	67			69	57	9	9				2		2	1	14	2			1	2			2	5						6	248
8	78	8		102	11	5		6						2	3	2								2						4	223
7	45			118	11	15	6	2								1								3			1		1	4	207
5	104	12	2	77	19	8	2	7	1										1					7						5	245
4	108	5	10	116	14	16	6								1	1	1	2						7				1		7	295
3	26	1	1	15	112	7	42	1	5		1		2		6	3		3	.	1			1	13			2			3	245
2	62			56	41	20	5	2	1		11	1	2		3	1			2	1			2	13	1	1	3			13	240
1	71		3	54	41	31	2	3			2				3	4	3	1	5				4	20			3			7	257

RESULTS

An analysis of the pollen is presented in table 1, in which the microfossils are classified according to a rough ecological and taxonomic scheme, and in which the number of grains or spores of each type is given for each sample from a profile. Although these tables are fairly obvious, certain items need some explanation.

The "dominant tree pollen" referred to in the introduction, and of which at least 150 were counted for each sample, are conceived as including pollen of all trees which probably entered the upper arborescent stratum of the forests represented in the sedimentation. Thus, of the tree-producing genera listed in the table, only *Alnus* and *Salix*, and the Ericaceae are excluded from this group, and *Pinus*, *Picea*, *Abies*, *Tsuga*, *Quercus*, *Carya*, *Castanea*, *Betula*, *Carpinus*, *Liquidambar*, *Tilia*, *Nyssa*, and *Fagus* make up its composition.

Some of the results of the analyses are more readily comprehended because the microfossils are classified according to the following groups:

I. Woody plants
  A. Dominant trees
    1. Coniferous genera
    2. Oak-hickory genera
    3. Mesophytic genera
  B. Edaphic trees and shrubs
II. Non-woody plants
  A. Flowering-plant families
  B. Spores
III. Undetermined
IV. Undeterminable

Under the heading of conifers are shown those winged pollen grains which were identified as to genus, excluding *Tsuga* which was placed with the mesophytes of the deciduous forest. Those winged pollen grains classified as "fragments" include all crushed or obscure grains not suitable for identification, and fragments of larger than half-grain size. In the summary table (table 2), where percentages are given, the fragments have been prorated among *Pinus*, *Picea*, and *Abies*. This seems a fair practice, better than to ignore them or to guess at their generic identity.

All the *Pinus* pollen grains which were observed in a suitable position were measured, as were many of the grains of *Picea* and *Abies*. The significance of these measurements is taken up in the discussion. The line labeled "undetermined" includes all pollen grains for which I have been unable to make generic or family determination. Those labeled "undeterminable" were either too distorted and obscure or were lying in an unsuitable position for determination.

In several cases no effort was made to identify the microfossil beyond the family (Ericaceae, Compositae), but for woody plants and some spores it

was usually not difficult to carry the determination to the genus. The identification of species has been attempted only for *Pinus* and *Abies*, and in each case with very interesting results.

DISCUSSION

Table 2 presents the results of the pollen analyses by genera and percentage composition, following well established practice. The percentages are computed on a basis of the dominant tree species alone. The justification for such a procedure is that it simplifies analysis and is more suggestive of the quantitative relations of the genera than when percentages are based upon all microfossils. Both of these tables are arranged according to the following ecological group totals: spruce-fir climax forest (*Picea, Abies*), pine subclimax forest (*Pinus* spp.), oak-hickory-chestnut climax forest (*Quercus, Carya, Castanea*), and mixed mesophytic climax forest (*Tsuga, Betula*, etc.). The theory is that the above grouping allows a ready interpretation of the fossils with respect to the vegetational types and climate that prevailed at the time of the sedimentation. This theory is based upon the climatic indicator value of certain forest types at the present time, and the assumption that the past must be understood, in part at least, in terms of the present.

Although there is considerable general truth in such assumptions and interpretations, it must immediately be understood that paleo-ecological interpretations are sometimes extremely hazardous. The spruce-fir climax as a whole is an excellent indicator of certain ecological conditions of the humid microthermal climate, but in studies of a fossil flora there may be considerable representation of these genera without their having any sharp climatic indicator value. For example, species of these genera persist as postclimax relics on bog surfaces and north-facing slopes long after the spruce-fir climate as such has ceased to prevail in an area, and the dominant vegetation has developed an entirely different cast.

The genus *Pinus* provides a perfect example of the critical problem faced by the pollen analyst. Pine-dominated forests and pine-oak mixtures in eastern North America are usually considered to represent less mesophytic conditions than the contiguous climaxes. One only needs a very slight knowledge of the modern genus *Pinus* to realize that its extreme ecological variety makes broad interpretations on a basis of generic determinations alone very uncertain. There are pine species associated with nearly every tree-dominated climax in North America. Their tolerances for temperature range all the way from *P. banksiana*, which extends to the far northern continental timber line, to *P. caribaea*, which goes into the subtropics. Their tolerances for moisture vary from the species of the semi-arid piñon-juniper forests to the white pines which require mesophytic conditions. In paleo-ecological studies, as in studies of modern vegetation, one needs very much to know

TABLE 2

	Ecological Groups													Group totals				
	A		B	C			D							A	B	C	D	
Sample number	Abies	Picea	Pinus	Quercus	Carya	Castanea	Tsuga	Betula	Carpinus	Liquidambar	Tilia	Nyssa	Fagus	Spruce-fir climax	Pine subclimax	Oak-chestnut climax	Mixed mesophytic climax	Number of grains
	Station I Mt Collins South																	
10			97.0	1.2		1.2		0.6							97.0	2.4	0.6	167
9		2.3	94.3	2.8			0.6							2.3	94.3	2.8	0.6	175
6	1.1	2.3	81.2	10.5	1.1	1.1	1.1	0.8	0.4					3.4	81.2	12.7	2.3	256
5	1.3	11.8	63.1	14.7	1.3	4.5	0.9	2.3						13.1	63.1	20.5	3.2	306
4	4.6	2.0	47.9	21.1	8.7	4.6	7.7	2.5	0.5					6.6	47.9	34.4	10.7	194
3	0.5	11.0	72.3	6.6	0.5	8.2		0.5						11.5	72.3	15.3	0.5	181
1		11.2	85.0	2.5		1.2								11.2	85.0	3.7		80
	Station II Mt Collins North																	
12			41.3	33.5	1.8	18.8		4.1		0.4					41.2	54.1	4.5	218
11			49.6	33.3	3.2	2.8		9.7	0.8	0.4					49.6	39.3	10.9	246
10			57.4	23.6	0.4	11.4	1.2	5.9							57.4	35.4	7.1	237
9	2.3	5.3	58.0	17.4	1.1	8.0		9.5						7.6	58.0	26.5	9.5	264
8			21.6	33.4	2.8	10.3		21.6	9.8	0.5					21.6	46.5	31.9	203
6	7.7		74.2	11.5	1.2	1.2		3.4	0.4	0.4				7.7	74.2	13.9	4.2	260
5			14.2	43.1	0.5	27.9		7.3	6.8						14.2	71.5	14.1	190
3	2.3		68.6	12.8	7.0	4.6	1.5	2.3	0.4		0.4			2.3	68.6	24.4	4.6	258
2			28.0	41.1	11.1	9.1		6.2	3.8		0.5				28.0	61.3	10.5	207
	Station IV Fingerville																	
10		3.0	29.6	33.1	23.1	7.0		2.0		1.0		1.0		3.0	29.6	63.2	4.0	199
9		2.7	55.4	24.3	3.6	9.4	1.8	2.7						2.7	55.4	37.3	4.5	222
8			60.2	25.5	10.4	0.8	2.1						0.8		60.2	36.7	2.9	231
7			68.2	17.5	10.0	1.4	0.5		0.5	0.9	0.9				68.2	28.9	2.8	211
6	7.6		53.6	23.8	9.4		1.8	0.9		1.8			0.9	7.6	53.6	33.2	5.4	222
5	17.0	7.6	49.3	15.9	5.1		4.2			0.8				24.6	49.3	21.0	5.0	235
4	14.2	2.2	60.4	11.1	7.5		4.0			0.4				16.4	60.4	18.6	4.4	225
3	6.3		72.7	8.0	7.1		3.3	1.2		0.4			0.8	6.3	72.7	15.1	5.7	238
2	13.9		52.2	12.4	10.1	1.5	5.6	1.5		0.4			2.2	13.9	52.2	24.0	9.7	266
1	13.7	2.9	52.5	9.2	9.6	2.5	7.5			0.4		1.6		16.6	52.5	21.3	9.5	240
	Station VIII Pauline																	
23			24.4	62.2	7.0	5.8							0.6		24.4	75.0	0.6	172
22	2.3	6.9	47.5	20.9	16.9	5.2								9.2	47.5	43.0		172
20			10.7	59.7	7.3	21.3							1.0		10.7	88.3	1.0	206
19			10.1	73.0	5.6	10.1						0.6	0.6		10.1	88.7	1.2	178
18			17.6	75.0	4.2					1.1		1.7			17.6	79.2	2.8	176
17			30.3	58.6	8.9	2.1									30.3	69.6		191
16			9.4	70.0	12.8	6.6							1.0		9.4	89.4	1.0	180
15			13.1	49.6	10.7	26.6									13.1	86.9		191
13			17.0	53.3	11.2	18.5									17.0	83.0		259
11		1.2	6.0	69.5	4.2	12.5		3.6		3.0				1.2	6.0	86.2	6.6	167
10			4.3	44.3	3.2	46.5		1.6							4.3	94.0	1.6	185
9			63.0	26.4	4.1	4.1				0.9		0.9	0.5		63.0	34.6	2.3	216
8		7.5	81.1	5.2	2.6		2.8						0.9	7.5	81.1	7.8	3.7	212
7			82.7	5.6	7.6	3.0	1.0								82.7	16.2	1.0	197
5	1.7	10.3	72.0	8.2	3.4	0.8	3.0	0.4						12.0	72.0	12.4	3.4	232
4	7.1	3.6	74.9	5.0	5.7	2.1	1.4							10.7	74.9	12.8	1.4	279
3	0.9	0.9	18.3	52.5	3.3	19.7	0.5	2.3		0.5		0.9		1.8	18.3	75.5	4.2	213
2			58.7	20.4	9.9	2.5	1.0	0.5		5.5	0.5	1.0			58.7	32.8	8.5	201
1	2.9		58.9	19.8	15.0	1.0	1.5			1.0				2.9	58.9	35.8	2.5	207

what the species are, for the ecological tolerance of different species of the same genus may be greatly different. Nevertheless, in eastern North America, when pine pollen is considered in relation to other genera, and to changes from horizon to horizon, certain interpretations as to the significance of the pine may be made on a basis of generic determination only.

Somewhat similar problems arise in connection with the oak-hickory and oak-chestnut associations. Different oak species have tolerances ranging all the way from some which require a moist condition, tolerate a saturated soil, and never constitute a portion of the climax association (*Q. palustris, Q. bicolor*), to others which are climax dominants and codominants of associations of various conditions (*Q. alba, Q. macrocarpa*), and several species of the western montane and foothill forests.

It is usually necessary in pollen studies to group several genera under the broad heading of mixed mesophytic forest, for it is nearly always impossible to distinguish in fossil floras whether the genera were actually present as an undifferentiated mesophytic type or as a series of association segregates. As a matter of fact, this grouping of mesophytic genera usually provides as much information as is useful in pollen analysis, for the technique does not allow much refinement of interpretation in many studies.

With these preliminary cautions, we may examine table 2 for such information as it may yield. In the first place, Spartanburg is in the Piedmont in an area usually classified on a basis of modern vegetation as oak-chestnut climax association or oak-pine. The element in the fossil flora that is distinctly out of climatic harmony is that of the spruce-fir climax. This element reaches maxima of 13.1 per cent in the fifth spectrum of Station I, 7.7 per cent in the sixth spectrum of Station II, 24.6 per cent in the fifth spectrum of Station IV, and 12.0 per cent in the fifth spectrum of Station VIII. Although the representation of spruce-fir is somewhat erratic from spectrum to spectrum, especially at stations II and VIII, it is apparent that most of these fossils occur in the lower levels of the buried soils and are absent or sporadic and of low percentage in the upper half of the sediments. One is immediately led to the conclusions that the climate was somewhat cooler at the time of sedimentation than at present, and that the period of time represented by the deposits included a retrogression of spruce-fir during the upper half.

These conclusions seem warranted despite the preponderance of non-spruce-fir pollen, providing, of course, it is assumed that the spruce and fir pollen grains were not blown to the sedimentary basins from a considerable distance where a different climate prevailed. Although there are no good data on this point, there are certain facts which in this case argue against the long-distance, wind-dissemination hypothesis. The representation of spruce-fir at certain horizons is too great for them to be considered made

up of grains transported a considerable distance. Today the spruce-fir climax occurs on the high southern Appalachians about 60–100 miles northwest of the Spartanburg deposits, and the prevailing winds blow from the southeast. If the climate was cooler at the time of sedimentation than now, the spruce-fir formation would probably have occurred on more of the southern mountains than at present and also have extended its lower limits to lower altitudes. There is nothing in the spectra, however, to indicate that a spruce-fir climate prevailed at Spartanburg at the time of sedimentation. It appears more reasonable to conclude that spruce and fir grew in and locally around the small ponds where the organic deposits accumulated, and that the upland was dominated by a mixture of oak-hickory-chestnut climax and pine subclimax. Taking the views described above, it seems necessary for us to assume that the spruce-fir in the Spartanburg region played the role of postclimax relics, and that the climate even earlier—at a time not represented by these four profiles—had been more like that of spruce-fir climaxes today. One would hazard, then, that the time represented by the buried soils was probably associated with one of the waning periods of the Pleistocene, but which one is unguessed.

The above conclusions do not rest only upon the evidence of the spruce and fir pollen. When the slides were being examined, measurements were made of several hundred pine grains. On a basis of size-frequency studies (Cain 1940), it appears that the smallest of the three fossil species from the buried soils was probably *Pinus banksiana*. If this determination is correct, and present information so indicates, jack pine is as good an indicator of the changed climate as spruce and fir, and these genera offer mutual corroboration. The pine with the small pollen has a considerable representation: 61 per cent at Station I (spectrum 10), 17 per cent at Station II (spectrum 6), 10 per cent at Station IV (spectra 2 and 9), and 12 per cent at Station VIII (spectrum 7). This species occurs generally at all levels in moderate amounts without indicating any discernible trend. Its strong representation at Station I appears to be exceptional. Furthermore, the idea of long distance dissemination which must be considered for spruce and fir is even more untenable for jack pine. Today it does not grow natively closer to Spartanburg, so far as published records reveal, than northern New York and northern Indiana. It is not known, of course, where this pine grew during the period of sedimentation, nor why it should have been completely eliminated from the area, but there is no pine known at present in the southeast with pollen grains so small. Sandy habitats are not abundant in the southern highlands, and an ameliorating climate might have resulted in rather rapid succession and the elimination of a species like jack pine through the competition of climax dominants.

In addition to the above conifers, it should also be noted that *Tsuga* is

today alien to the prevailing climate, and that the more mesophytic trees (*Fagus, Betula,* etc.) are confined, as postclimax relics, to protected ravines and slopes. Finally, the presence of *Sphagnum* spores in each buried soil, and their considerable numbers at Station I, are in accord with the preceding interpretations.

With respect to these considerations, I believe a reconstruction of the vegetation during the time of sedimentation would be somewhat as follows. The characteristic upland climax, probably occupying the largest acreage, was oak-hickory-chestnut. This climax was probably interrupted in many places by pine subclimax—on drier, rockier, upper slopes and, especially, where fires had destroyed the climax. Generally through the area, but especially in the ravines and on the protected slopes of the stream systems, occurred the mixed mesophytic forests playing, even at this time, a postclimax role. Finally, on the local ponds where the buried soils accumulated, there probably grew most of the spruce and fir. They probably occurred as bog-mat species and on the cooler slopes adjacent to the ponds. The general picture, then, is not much different from that which probably prevailed before man and his agriculture except that the climate was sufficiently cooler, especially in the earlier part of the period, to have supported spruce-fir, jack pine, etc., now absent. How much cooler it is not possible to say, since these cool-climate elements already occurred solely as relics out of harmony with the prevailing conditions and depending for their survival upon edaphic and microclimatic conditions.

Returning to the question of the identification of species in fossil floras, there are certain points that must be emphasized. Specifically, it can not be assumed as proven that the Spartanburg sediments contain pollen of *Pinus banksiana.* It has been shown only that certain abundant small grains in the sediments resemble closely grains of that species. The grains of *Abies* are likewise of special interest. It was at first assumed, and reasonably so, that the fir pollen of the sediments was *Abies Fraseri,* the modern species of the high southern Appalachians. A recent study (Cain 1944), however, has shown that the fossil fir pollen does not correspond in size with *Abies Fraseri* or *A. balsamea,* but is very much larger and more like the western *A. nobilis* (Wodehouse 1935). Although such a study does not serve to identify the fossil *Abies,* it does away with what would otherwise appear to have been a logical guess as to its identity. Perhaps the fir pollen is that of an extinct species rather than of one that is now geographically far distant. In the same manner, the small-grained pine may be an extinct species, rather than the far-northern jack pine. In any case, we are given a suggestion that the buried soils are possibly of greater age than early post-Wisconsin, for it is unusual for post-Wisconsin sediments to contain extinct species, or for ex-

tant species to have withdrawn their areas such great distances as would be required in the case of this pine and fir.[3]

Attention must also be given to certain other aspects of the profiles. At Station I the oak-hickory-chestnut complex shows a consistent rise and decline from the bottom to the top of the buried soil, with a maximum of about 35 per cent in the spectrum of level number four. This curve is paralleled by a similar but weaker one for the combined mesophytes. No such simple curve is apparent in the other profiles. At Station IV there is a rather steady representation of the oak-hickory-chestnut complex of about 20 per cent in the lower half, with a generally progressive increase in the upper half to a maximum of 63 per cent at the top. This trend is not reflected by the mesophytes. At Station II, however, there is definite evidence that the oak-hickory-chestnut complex and the mesophytes show similar sensitivity to changed conditions. At levels 2, 5, 8, and 11 these groups increase together. Similarly, at levels 3, 6, and 9, when oak-hickory-chestnut decreases, the mesophytes do likewise. The correlation is not perfect, however, as can be seen from the tables.

One of the most interesting phenomena of the profiles is revealed at Stations II and VIII where there are abrupt, reciprocal changes in the importance of the pines and the oak-hickory-chestnut climax. For example, at Station II this climax drops from 62 to 24 per cent between levels 2 and 3, from 72 to 14 per cent between levels 5 and 6, and from 47 to 27 per cent between levels 8 and 9. These changes are balanced very largely by increases in the pines from 28 to 69 per cent, 14 to 74 per cent, and 22 to 56 per cent, respectively. This same tendency is shown at Station VIII, but in a less dramatic manner.

Because many pine species play a characteristic role as subclimax dominants following fire, it is suggested as a likely hypothesis that these alternations represent the widespread destruction of the oak-hickory-chestnut climax by fire and its replacement by an abundance of pine. This idea is supported by the presence of burned wood fragments and traces of charcoal at various levels in the sediments. There is no reason to believe, however, that the periods of time between the levels dominated by the oak-hickory-chestnut climax at levels 2, 5, and 8 (Station II) represent the time required for the recovery of the climax after its destruction by fire and replacement by pine. It is entirely unknown how long was required for the accumulation of a unit of sediment, but it is likely that nine inches of the peaty soil required a longer period of time than one cycle of recovery of the climax from fire.

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[3] An attempt at the specific identification of other fossils such as *Picea, Quercus, Carya,* etc., in these buried soils is recognized as highly desirable, but I have had no opportunity so far to go beyond the present studies.

So far in the United States there has been only a small number of paleontological studies depending upon pollen analysis made south of the continental moraines. I have materials for the study of other profiles in the Spartanburg area, but there are large numbers of these buried soils elsewhere, and they should be sought through a wider portion of the Piedmont so that a greater abundance of information will be available for correlation studies and attempts at dating. It is hoped also that investigators will devote increasing attention to the possibility of identification of species and the breaking down of the customarily large ecological groupings of pollen grains and spores. The recent study of grass pollen by Keller (1943) is an excellent step in that direction. So far I have made no attempt to utilize macrofossils from these profiles for corroboration and supplementation of the pollen studies, but it should be done when time permits. And not only should pollen analysts supplement their pollen investigations with study of whatever macrofossils may be available: there are famous fossil floras, up to now examined solely on a basis of macrofossils, awaiting examination by enterprising pollen analysts. The work of Wodehouse (1932) on the pollen grains of the Green River flora is the only one of such scope yet made in the United States so far as I know.

SUMMARY

In the Piedmont near Spartanburg, South Carolina, there are numerous small sedimentary basins containing highly organic soils that are buried under several feet of inorganic soil of types generally considered to be completely residual. Pollen analyses of profiles of four of these buried soils indicate that their age is sufficient to relate them to a cooler climate than prevails in the area today and probably to the Pleistocene. Pollen grains of *Picea* and *Abies* are more abundant in the lower half of the deposits, a fact that provides an indication that the sediments accumulated under a warming climate. It is demonstrated that the *Abies* is not one of the modern species of Eastern America, and that one of the pines may be the northern *Pinus banksiana*. On a basis of these data it is concluded that the burial of the soils was probably not associated with accelerated erosion in historical times due to agriculture.

The profiles reveal some indication of repeated destruction of the oak-hickory-chestnut climax by fire, its replacement by pine, and its recovery again to climax conditions.

The general picture of the vegetational pattern of the Spartanburg area during the time of the sedimentation is as follows: The rolling uplands were covered by a climax of oak-hickory-chestnut; ravines and protected slopes contained stands of mixed mesophytes; several places where small streams were impounded postclimax spruce-fir grew on and around bog-like basins;

over the upland the prevailing climax was interrupted by stands of pine and pine-hardwood mixtures representing various stages of secondary succession.

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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 71, NO. 1, PP. 23–45 JANUARY, 1944

THE VEGETATION OF PILOT MOUNTAIN, NORTH CAROLINA: A COMMUNITY ANALYSIS[1]

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INTRODUCTION

Rising abruptly to a height nearly 1500 feet above its surroundings, Pilot Mountain has long been a landmark in the northwestern Piedmont of North Carolina. Although it is located well within the Piedmont Plateau and is isolated from the Blue Ridge, certain species that are ordinarily found only at high altitudes occur near its summit. These obvious relationships both to the Piedmont and to the mountains proper suggested the desirability of an ecological study, and a phytosociological survey of the vegetation was made in 1941 and 1942.

THE AREA

Pilot Mountain is the most southwestern outpost of the Sauratown Mountains and is located in the southeastern corner of Surry County, North Carolina. Several miles separate it from the two nearest spurs of the Sauratown Range. Except for hills in its immediate vicinity, the 2413 foot peak (Pratt 1917) is isolated and is surrounded by the characteristic gently rolling topography of the Piedmont Plateau.

Topography. The mountain may be separated topographically and vegetationally into two distinct parts. The eastern half is an almost perfect pyramid, which is topped by The Knob, or Big Pinnacle (fig. 1); the western half is an elongated, gently rounded ridge, which, extending westward from its highest point, the Little Pinnacle, is outlined by The Ledge. Both The Ledge and the sides of the two pinnacles are nearly vertical cliffs composed of horizontally stratified rock.

On the north the two sections of the mountain are separated by Grindstone Ridge, which slopes gradually downward from the Little Pinnacle. A third long ridge extends downward from the southeast corner of The Knob, and several shorter ones are found on all exposures. Northwest of the Big Pinnacle, separating it from the Little Pinnacle and from Grindstone Ridge, is a broad cove, which is dissected by several shallow ravines and broad, low ridges. A number of ravines occur on the eastern half of the mountain, but few are found on the western half.

There are several flats at various altitudes on the eastern pyramid. The two largest, both at about 1600 feet, are Hickory Flat, which extends across

[1] Publication of the tables is made possible by a grant from Duke University.

most of the east slope, and Poplar Flat, which covers fifteen or more acres on the south slope.

Geology and Soils. Descriptions which follow are based upon the soil survey of Surry County (Davis and Goldston 1937), the only available record that deals specifically with geology and soils of the area.

Quartzite caps Pilot Mountain, and hornblende schist occurs intermixed with gneiss along its western boundary. At all altitudes small outcrops of

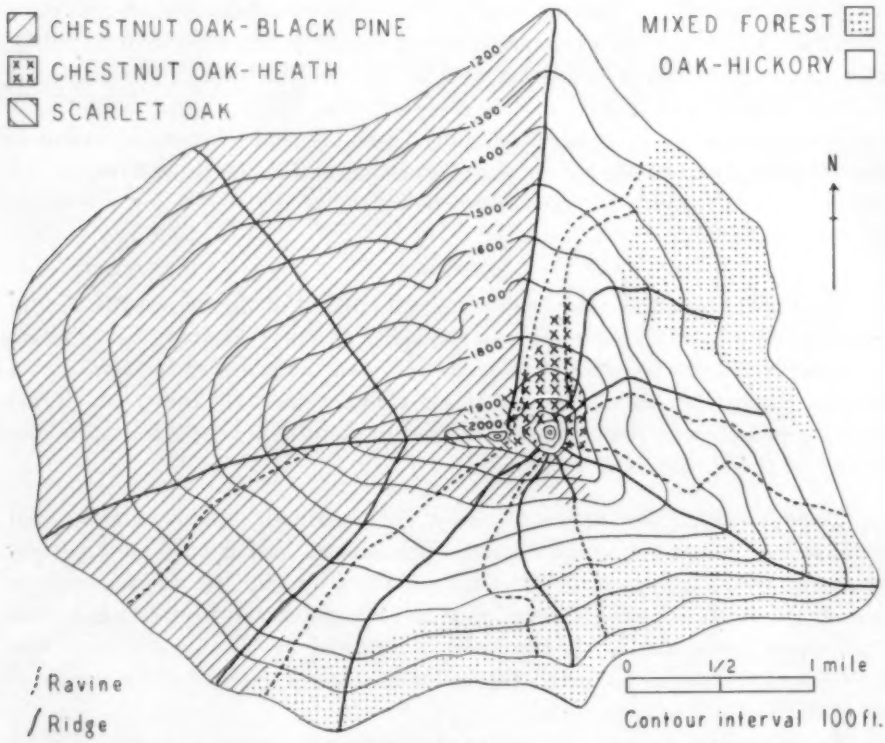

FIG. 1. Rough contour map of Pilot Mountain showing positions of transect lines and general extent of each major plant community. Contours adapted from Book 69, office of Register of Deeds, Dobson, N. C.

quartzite are numerous, and many slabs are scattered over the surface. The soils are derived from the underlying quartzite. Hartsells stony fine sandy loam occurs at the lower altitudes, and its steep phase, interrupted by rock ledges and outcrops, covers the steeper slopes. On gentle slopes the surface soil (A horizon) is from 5 to 8 inches thick and is a light gray to grayish-yellow fine sandy loam. In places organic accumulation produces a brown color. The subsoil (B horizon) is a pale yellow or grayish-yellow friable fine

sandy loam which grades into the yellow, disintegrated quartzite at a depth ranging from 15 inches to 4 feet. On the steep slopes and on most of the western half of the mountain the veneer of soil is very thin. A restricted area on the north slope below The Knob has a red soil with a brown surface (Hanceville).

Climate. The nearest weather station is at Mount Airy, which is some twenty miles from Pilot Mountain and which has an altitude of only 1048 feet. The average annual precipitation there is 46.69 inches, with the greatest rainfall recorded for the summer months and the least, for November. The mean annual temperature is 56.9° F. Monthly averages vary from 75.3° F for July to 38.0° F for January. Other stations in this section have similar records with very minor variations.

Although climatological data are not available from The Pilot itself, or from a comparable locality in its vicinity, it is only logical to assume that the precipitation and temperature on the mountain follow the same monthly trends as those recorded at nearby stations; but that the precipitation is somewhat greater on the mountain, while the temperature is slightly less. The growing season is also evidently less than the average frost-free season of 175 days recorded at Mount Airy.

History. Exploitation of the resources and scenery of Pilot Mountain has been attempted by its several owners with but meager success. At times every tree of merchantable size has been cut for lumber. Recently, however, the only cutting has been of cordwood from around the base. Several orchards and cleared fields are found on the lower slopes, and there are indications that a number of others once existed but have been abandoned. As recently as 1930, a field was cleared on top of The Ledge, but it was abandoned after a few years of unsuccessful cultivation.

Teresa Gilliam, for whom the mountain and surrounding lands were held in trust from 1826 to 1870, seems to have realized that the chief values of The Pilot are scenic. She had a trail constructed on the south side of the mountain and ladders on the side of The Knob. No further serious attempt to commercialize the mountain was made until 1929, at which time Mr. Spoon built wooden steps on the north side of the Big Pinnacle and constructed a toll road from the base of the mountain on the northeast to the summit of the Little Pinnacle.

Fire occurred very regularly in the past and resulted in extensive burned-over areas. The most serious recent fire burned over most of the mountain in 1927, and practically all of the large trees are badly fire-scarred. Since the construction of the toll road, however, only two small fires have occurred.

METHODS

The known collections from Pilot Mountain include 303 species of vascular plants representing 76 families. Collections of mosses, though incomplete, include 55 species representing 16 families. All these specimens are deposited in the herbarium of Duke University.

A statistical study was based upon 158 sample areas (stations), which were spaced at altitudinal intervals of 100 feet along lines (fig. 1) ascending 9 slopes and 8 ravines. Although the samples were taken at intervals the vertical lines were considered as modified transects. At each station estimates were made of *abundance*, *coverage*, *size classes*, and *sociability* of each species on an area approximately 50 feet square. The transect plan was originally used because altitudinal variation in the vegetation was anticipated. However, when the results had been tabulated and compared with habitat notes taken at each station, it was found that four general plant communities exist on Pilot Mountain. The limits of these communities were defined (fig. 1), and the data were separated accordingly. From these statistics a sociological summary of each community was made.

In general, the terminology used is that which was summarized by Cain (1932). The vertical "transect" lines were treated as stands and the altitudinally spaced stations were used as sample areas within the stands. The average frequency of each species within a community was obtained by averaging the frequency values for that species from all "transects" or portions of "transects" that fell within the boundaries of the community under consideration. The results are expressed in percentages. Similarly, values for abundance and coverage were averaged. These values, however, are expressed by means of classes. For abundance, the 5 classes suggested by Cain (1932) were used. For coverage, a class was added for the species that occupy less than one per cent of the surface; thus giving the following arrangement:

C 0, species covering less than 1 per cent of the surface.
C 1, species covering 1–5 per cent of the surface.
C 2, species covering 6–25 per cent of the surface.
C 3, species covering 26–50 per cent of the surface.
C 4, species covering 51–75 per cent of the surface.
C 5, species covering 76–100 per cent of the surface.

The five size classes that were recognized are:

S 1, species found in the ground cover.
S 2, herbs and shrubs below one foot in height.
S 3, shrubs and transgressives below 8 feet in height.
S 4, trees of the understory.
S 5, trees of the upperstory.

Presence is expressed as a percentage which indicates the ratio of the number of stands ("transects") in which the species occurred to the number

of "transects" placed within the community. The values for constancy are based upon the total number of sample areas (stations) which were studied in a community. Five classes of constancy are recognized and those species which occurred at more than 80 per cent of the stations (class 5) are considered to be constants. The classes are as follows:

Co 1, species occurring in 1–20 per cent of the examples.
Co 2, species occurring in 21–40 per cent of the examples.
Co 3, species occurring in 41–60 per cent of the examples.
Co 4, species occurring in 61–80 per cent of the examples.
Co 5, species occurring in 81–100 per cent of the examples.

DESCRIPTION OF COMMUNITIES

Most extensive of the four plant communities on Pilot Mountain is the *chestnut oak—black pine* community of the western half of the mountain and the upper south slopes. This gradually changes into the *chestnut oak—heath* of the higher east and north slopes. Richest and most heterogeneous of the four is the *oak-hickory* forest of the middle altitudes and ravines on the south, the east, and the north-facing slopes that lie below The Knob. The *mixed forest* occupies the lower slopes of these exposures. Because of its position and peculiar flora the *top of The Knob* is treated separately.

Chestnut Oak—Black Pine Community. Except for ravines, this community occupies all the area from Grindstone Ridge westward around the mountain to that ravine on the south which separates the two pinnacles. It also continues across that part of the south-facing slope which roughly lies between an altitude of 1800 feet and The Knob, and gradually gives way to the chestnut oak—heath (fig. 1).

Most of this region has a gently rounded slope with but few ridges and ravines. A thin layer of soil only partially covers the rocky surface, and the poor quality of the site is reflected in the vegetation. The trees are poorly developed and form an open canopy, while the shrubs and herbs are scattered and frquently appear stunted.

Data from 61 stations distributed along 11 "transects" are summarized in table 1. These show seven constants: *Quercus montana*[1] and *Pinus rigida* in the tree layer, *Quercus marilandica* and *Oxydendrum arboreum* in the understory, *Vaccinium vacillans* and *Kalmia latifolia* in the shrub layer, and *Andropogon* spp. in the herb layer. If *Nyssa sylvatica*, chiefly an understory species whose frequency is 87 per cent, were included with the seven constants, this list would contain all species with abundance values of 4 or 5, or average frequencies of more than 80 per cent. Except for *Oxydendrum arboreum*, each of these species has a presence of 100 per cent.

[1] Authorities for names are given in the tables the first time each specific name appears.

TABLE 1

Data for Chestnut Oak—Black Pine Community with Stratification (S), Abundance (A), Coverage (C), Frequency (F), Presence (P), and Constance (Co) for each species

Species	S	A	C	F	P	Co
Usually found in upperstory:						
Quercus montana Willd.	5, 4, 3	5	2	97	100	5
Pinus rigida Mill.	5, 4, 3	5	2	96	100	5
Quercus coccinea Muench.	5, 4, 3	3	1	42	64	3
Pinus virginiana Mill.	5, 4, 3	2	0	17	36	2
Pinus pungens Lam.	5, 4, 3	2	0	18	64	1
Quercus velutina Lam.	5, 4	2	0	9	36	1
Quercus alba L.	5, 4	1	0	6	18	1
Pinus echinata Mill.	5, 4	1	0	3	18	1
Liriodendron tulipifera L.	5, 4, 3	1	0	1	18	1
Usually found in understory:						
Quercus marilandica Muench.	4, 5, 3	4	1	84	100	5
Oxydendrum arboreum (L.) DC.	4, 3, 5	4	1	94	91	5
Nyssa sylvatica Marsh.	4, 3, 5	4	1	87	100	4
Robinia pseudo-acacia L.	4, 2, 5	2	1	44	100	3
Sassafras albidum (Nutt.) Nees	4, 3, 2	2	0	51	82	3
Acer rubrum L.	4, 3, 5	2	1	39	82	3
Carya alba (L.) Koch, *C. glabra* (Mill.) Spach., *C. pallida* (Ashe) Sarg.	4, 3, 5	2	0	30	73	2
Castanea dentata (Marsh.) Borkh.	4, 3	2	0	34	64	2
Hamamelis virginiana L.	4, 3	1	0	6	36	1
Amelanchier canadensis (L.) Medic.	4	1	0	4	27	1
Quercus borealis Michx. var. *maxima* (Marsh.) Ashe	4	1	0	1	18	1
Shrub layer:						
Vaccinium spp.	2, 3	5	1	99	100	5
Kalmia latifolia L.	3	4	2	84	100	5
Polycodium stamineum (L.) Greene	3, 2	2	1	45	82	3
Azalea nudiflora L.	3, 2	2	1	33	82	2
Gaylussacia baccata (Wang.) K. Koch.	2, 3	2	1	40	73	2
Diospyros virginiana L.	3, 4	2	0	32	82	1
Epigaea repens L.	1	2	0	23	55	1
Ilex montana (T. and G.) Gray	3	1	0	17	45	1
Ceanothus americanus L.	3, 2	1	0	12	36	1
Quercus ilicifolia Wang.	3	1	0	10	36	1
Lyonia ligustrina (L.) DC.	3	1	0	9	36	1
Comptonia peregrina (L.) Coult.	2	1	0	9	36	1
Robinia hispida L.	2	2	0	8	36	1
Rhododendron catawbiense Michx.	3	1	0	9	27	1
Rubus spp.	3, 2	1	0	6	27	1
Rhus copallina L.	3	1	0	11	18	1
Galax aphylla L.	1	1	0	4	18	1
Rhododendron maximum L.	4	1	0	2	18	1
Rhus glabra L.	3	1	0	2	18	1
Castanea pumila (L.) Mill.	3	1	0	5	9	1
Woody vines:						
Smilax rotundifolia L.	3, 2, 4	3	1	65	100	4
Vitis aestivalis Michx. and *V. cordifolia* Michx.	4, 3	1	0	1	18	1

TABLE 1 (*Continued*)

Species	S	A	C	F	P	Co
Herbs:						
Andropogon scoparius Michx. and *A. virginicus* L.	2	4	1	89	100	5
Pteridium aquilinum (L.) Kuhn, 2 var.	2	3	1	75	100	4
Chrysopsis graminifolia Nutt. var. *aspera* (Shuttlew.) Gray	2	2	0	67	100	4
Panicum spp.	2	2	0	60	100	3
Leguminosae spp.	2	3	1	63	91	3
Solidago spp.	2	2	0	62	91	3
Tephrosia virginiana (L.) Pers.	2	3	1	59	91	3
Coreopsis major Walt.	2	2	0	38	82	3
Hieracium venosum L.	2	2	0	48	100	2
Iris verna L.	2	2	0	16	45	2
Seriocarpus asteroides (L.) BSP.	2	1	0	12	55	1
Baptisia tinctoria (L.) R. Br.	2	1	0	17	45	1
Houstonia tenuifolia Nutt.	2	2	0	16	45	1
Potentilla spp.	2, 1	1	0	9	34	1
Hypoxis hirsuta (L.) Coville	2	1	0	5	27	1
Viola spp.	2	1	0	4	27	1
Chimaphila maculata (L.) Pursh	2	1	0	3	27	1
Silphium compositum Michx.	2	1	0	3	27	1
Euphorbia corollata L.	2	1	0	3	18	1
Gillenia trifoliata (L.) Moench.	2	1	0	3	18	1
Gramineae sp.	2	1	0	2	18	1
Aureolaria spp.	2	1	0	1	18	1
Smilacina racemosa (L.) Desf.	2	1	0	1	18	1
Compositae spp.	2	1	0	7	9	1

NOTE: The following species occurred in only one station and therefore have a constance of two per cent and a presence of nine per cent: *Antennaria* sp., *Aralia spinosa* L., *Asarum* sp., *Asplenium platyneuron* (L.) Oakes, *Galium* sp., *Hypopitys americana* (DC.) Small, *Osmunda cinnamomea* L., *Phoradendron flavescens* (Pursh) Nutt., *Polygonatum biflorum* (Walt.) Ell., *Polypodium virginianum* L., *Polystichum acrostichoides* (Michx.) Schott., and *Sagina decumbens* (Ell.) T. and G.

Sixteen additional species have a presence of more than 80 per cent, but only 8 of these have a cover value of as much as 1 per cent: *Robinia pseudo-acacia* and *Acer rubrum* in the understory; *Polycodium stamineum*, *Azalea nudiflora*, and *Smilax rotundifolia* among the shrubs; *Pteridium aquilinum*, *Tephrosia virginiana*, and several other legumes among the herbs. Of this supplementary list, only *Pteridium aquilinum*, *Smilax rotundifolia*, and the legumes have frequencies that average more than 50 per cent.

Some oaks and pines in the upperstory appear to be dying, and a number of the older oaks are grotesquely gnarled. Of the upperstory species, chestnut oak is by far the most important in lesser strata. Blackjack oak seldom attains upperstory size but often occurs in dense stands. These two oaks dominate the understory and transgressive layers, with sourwood and black gum as important associates. Seedlings of both oaks are numerous, and black locust, though widely scattered in the understory, is often found among the

TABLE 2

Data for Chestnut Oak—Heath Community with Stratification (S), Abundance (A), Coverage (C), Frequency (F), Presence (P), and Constance (Co) for each species

Species	S	A	C	F	P	Co
Usually found in upperstory:						
Quercus montana	5, 4	5	1	91	100	5
Pinus rigida	5, 4	4	1	69	88	4
Pinus pungens	5, 4, 3	2	0	17	25	2
Quercus borealis var. *maxima*	5, 3	1	0	27	38	1
Usually found in understory:						
Nyssa sylvatica	4, 3	3	1	61	100	4
Castanea dentata	4, 3	3	1	80	88	4
Oxydendrum arboreum	4, 3, 5	3	1	69	88	4
Robinia pseudo-acacia	4, 2	2	0	63	88	3
Acer rubrum	4, 3	2	0	56	75	3
Hamamelis virginiana	4, 3	2	0	54	75	3
Sassafras albidum	4, 3	3	1	48	75	3
Carya spp.	4	1	0	27	38	1
Amelanchier canadensis	4	1	0	13	25	1
Shrub layer:						
Kalmia latifolia	3, 4	5	2	100	100	5
Rhododendron catawbiense	3, 4	4	1	83	100	5
Vaccinium spp.	3, 2	4	1	71	100	5
Epigaea repens	1	3	1	76	100	4
Gaylussacia baccata	3, 2	4	1	72	100	4
Lyonia ligustrina	3	2	0	52	75	3
Galax aphylla	1	3	1	45	75	3
Leucothoe recurva (Buckl.) A. Gray	3	2	0	35	75	2
Quercus ilicifolia	3	2	0	35	75	2
Polycodium spp.	3	2	0	30	63	2
Pieris floribunda (Pursh) Benth. & Hook	3	2	1	21	25	2
Azalea nudiflora	3	2	0	25	38	1
Ilex montana	3	1	0	17	38	1
Aronia melanocarpa (Michx.) Ell.	3	1	0	14	38	1
Comptonia peregrina	2	1	0	10	25	1
Woody vine:						
Smilax rotundifolia	3	2	0	27	50	2
Herbs:						
Pteridium aquilinum, 2 var.	2	2	0	44	75	3
Solidago spp.	2	2	0	46	88	2
Andropogon spp.	2	2	0	43	38	1
Chrysopsis graminifolia var. *aspera*	2	1	0	23	38	1
Osmunda cinnamomea	2	2	0	21	38	1
Iris verna	2	1	0	23	38	1
Baptisia tinctoria	2	1	0	23	25	1
Gramineae sp.	2	1	0	17	25	1
Leguminosae spp.	2	1	0	17	25	1
Panicum sp.	2	1	0	17	25	1
Deschampsia flexuosa (L.) Trin.	2	1	0	16	25	1
Chimaphila maculata	2	1	0	14	25	1
Polystichum acrostichoides	2	1	0	14	25	1
Seriocarpus asteroides	2	1	0	13	25	1
Asarum sp.	2	1	0	10	25	1
Aureolaria spp.	2	1	0	10	25	1

TABLE 2 (*Continued*)

Species	S	A	C	F	P	Co
Paronychia argyrocoma (Michx.) Nutt.	2	1	0	10	25	1
Polypodium virginianum	2	1	0	10	25	1
Gillenia trifoliata	2	1	0	6	25	1
Dioscorea glauca Muhl.	2	1	0	8	13	1

NOTE: The following species occurred in only one station and therefore have a constance of five per cent and a presence of thirteen per cent: *Asplenium platyneuron, Athyrium asplenioides* (Michx.) Desv., *Diospyros virginiana, Euphorbia corollata, Goodyera pubescens* R. Br., *Heuchera* sp., *Hieracium venosum, Houstonia tenuifolia, Hydrangea arborescens* L., *Liriodendron tulipifera, Polygonatum biflorum, Pyrus malus* L., *Quercus coccinea, Quercus marilandica, Smilacina racemosa, Steironema intermedium* Kearney, *Tephrosia virginiana,* and *Viola pedata* L.

seedlings. Sassafras is important in the understory on the higher south slopes. Although colonies of young pines frequently occur in openings, pine, when the entire area is considered, is of less importance in the lower strata than are the hardwoods. The shrub layer is composed chiefly of huckleberries, laurel, and transgressives. It seems to be better developed on north-facing than on south-facing slopes, and its importance also increases with altitude. Scattered herbs are present everywhere except in the dense stands of blackjack oaks.

The greatest variation in the community occurs in the triangular area that lies between Grindstone Ridge and The Ledge. Here scarlet oak not only replaces blackjack oak but in places almost crowds out chestnut oak and pine. Since the area concerned is small, and since the subordinate species are not different, this evidently constitutes a local variation of the chestnut oak—black pine community.

Minor local variations are related to more favorable moisture conditions. In such places service berry, rhododendron, mountain holly, bear oak, galax, and cinnamon fern may be found, while the usual shrubs are larger and more abundant. In crevices and pockets on the rock cliffs that form the sides of the two pinnacles and The Ledge, are found certain species that are seldom seen elsewhere on the mountain: namely, *Asplenium montanum* Willd., *Heuchera parviflora* Bartl. var. *typica* R., B. and L., *Sagina decumbens,* and *Paronychia argyrocoma.* Along with these are various other plants, even dwarf trees.

Chestnut Oak—Heath. The chestnut oak—heath extends along both east and north-facing slopes immediately below The Knob but reaches its best development at the north base and down a shallow ravine on the north side (fig. 1). Although scattered ericads may be present in the shrub layer at lower altitudes, their occurrence in thickets is infrequent below an elevation of 1900 feet. The ravine on the north is an exception, for there the heath

thicket extends downward almost 200 feet farther than its usual limit. Throughout most of the area occupied by this community the slope is steep and rocky, with thin soil and litter only in spots.

Vegetational statistics were secured from 20 stations distributed along 8 "transects." The data (table 2) show that the constants, in order of their decreasing abundance and frequency are: *Kalmia latifolia*, *Quercus montana*, *Rhododendron catawbiense*, and species of *Vaccinium*. The first three are the only species in this community with average frequencies of over 80 per cent, but each constant has a presence of 100 per cent. Since the shrubs are more abundant than the trees and have a greater coverage, in places approaching 100 per cent, and since 7 of the 12 shrubs that have frequencies of more than 20 per cent are ericads; the name "chestnut oak—heath" seems most appropriate for the community.

In general, the physiognomy is that of dwarfed, widely spaced trees above a dense thicket of shrubs and trees that are scarcely taller than the shrubs. Chestnut oak is the dominant tree, but clusters of pine occur in places where the laurel and rhododendron are replaced by huckleberries. All the trees are of fair size at lower altitudes but rapidly decrease in number, size, and quality as The Knob is approached. At the base of The Knob, the trees are dwarfed, and the shrubs are frequently from 8 to 12 feet high, while understory species are but slightly taller than the shrubs. This makes the three strata almost the same height.

In the understory is a greater number of chestnut sprouts than is found in any other community. Sourwood, black gum, and sassafras are fairly abundant. Transgressives and seedlings of tree species are found in openings only, but seedlings of the shrub species are fairly abundant everywhere. The larger rocks form practically the only bare places, and even these are often partially or entirely obscured by the ericads. Laurel and rhododendron grow in clumps with many sprouts from the roots. Where these clumps are close together a true thicket is formed; where they are more widely spaced the other shrubs are usually as dense but not so tall as these two species. Bear oak forms its own thickets, which are evenly distributed through the upper altitudes. Huckleberries cover whatever space is left between the other shrubs and fill all openings in the thickets. Beneath all else is a carpet of galax or, at lower altitudes, trailing arbutus. Bracken fern is found here and there, but herbs are of little importance except in the paths.

Altitudinal zonation is apparent in the distribution of the shrubby plants of the community. The number of shrub species increases upward. At lower altitudes, varying from about 1725 feet in the north ravine to 1950 feet on the east, azalea, laurel, and huckleberries are the most important shrubs. Rhododendron and trailing arbutus enter at slightly higher altitudes; galax becomes abundant about 100 feet above the first colonies of

arbutus; and bear oak occurs still higher on the slope. Four species are found only in the chestnut oak—heath. *Leucothoe recurva* occurs for a short distance below The Knob, but *Pieris floribunda, Vaccinium corymbosum* L. var. *pallidum* (Ait.) Gray and *Aronia melanocarpa* are limited to the north base of The Knob and to its top. The *Pieris* is so abundant around the northwest base of The Knob that it is dominant, with a coverage of over 50 per cent.

Oak-Hickory Forest. This forest occupies middle slopes on the eastern half of the mountain and most ravines on all exposures. On the south-facing slopes, the transition from the lower mixed forest to oak-hickory coincides with a sudden increase in degree of slope at an altitude of about 1500 feet. The upper limit on this side is an abrupt transition to the chestnut oak—black pine community at about 1800 feet. On the east and north, the community extends from the chestnut oak—heath downward almost to the base of the mountain, where it is interrupted by agricultural land.

The topography is variable. Included are several flats, and drainage lines range from slight depressions to steep-walled ravines. In some areas the soil is deep and is rich in humus; in others, there are piles of nearly bare rock.

The diversity of conditions is reflected in the large number of species, 140 in all, listed from the 61 stations in 13 stands (table 3). *Robinia pseudoacacia*, with a frequency of 94 per cent, is the only constant; but *Vitis aestivalis*, which is the usual grape (frequency 80 per cent), probably deserves the same rating. When combined, oaks have a constancy of 95 per cent, and hickories of 90 per cent. *Liriodendron tulipifera* (frequency 80 per cent) is probably the most abundant single species in the community. It is local in occurrence, however, and cannot be considered a constant. An almost pure stand occupies about fifteen acres on Poplar Flat; the species is often dominant in the ravines; and small groups are scattered over the slopes, seemingly without design. In general, it is more common on south-facing slopes than on the east or north.

Among the oaks, chestnut oak is most important, having an abundance of 4 and an average frequency of 73 per cent. It becomes the dominant species at higher altitudes, particularly on the east and north. There the oaks are regularly and widely spaced and attain their best development. Northern red oak (frequency 64 per cent) is usually found in moister sites, while white oak (frequency 62 per cent) is more abundant in drier sites.

The understory is usually dense, and its most important species are transgressives that vary with the local dominants. Scattered among these, however, are other species, whose identities also vary with the sites. Sourwood, red maple, chestnut sprouts, and dogwood are more abundant on the east and north-facing slopes than on the south. Black gum, black locust, and per-

TABLE 3

Data for Oak—Hickory Community with Stratification (S), Abundance (A), Coverage (C), Frequency (F), Presence (P), and Constance (Co) for each species

Species	S	A	C	F	P	Co
Usually found in upperstory:						
Carya spp.	5, 4, 3	4	1	97	100	5
Robinia pseudo-acacia	5, 4	4	1	94	100	5
Liriodendron tulipifera	5, 4, 3	4	1	80	100	4
Quercus montana	5, 4, 3	4	1	73	100	4
Quercus borealis var. *maxima*	5, 4, 3	3	1	64	100	4
Quercus alba	5, 4, 3	3	1	62	100	3
Juglans nigra L.	5, 4	2	0	52	92	3
Pinus virginiana	5, 4	1	0	13	46	3
Quercus velutina	5, 4	1	0	15	54	1
Pinus rigida	5, 4	1	0	11	31	1
Pinus echinata	5, 4	1	0	7	23	1
Pyrus communis L.	5	1	0	1	8	1
Usually found in understory:						
Nyssa sylvatica	4, 5, 3	3	0	65	100	4
Diospyros virginiana	4, 3	1	0	48	92	3
Oxydendrum arboreum	4, 3, 5	2	0	53	85	3
Cornus florida L.	4, 5, 2	3	0	52	85	3
Acer rubrum	4, 5	2	0	50	85	3
Castanea dentata	4, 5	2	0	34	70	3
Fraxinus americana L. and F. *biltmoreana* Beadle	4, 5	2	0	58	62	3
Cercis canadensis L.	4, 5	2	0	35	62	2
Ulmus fulva Michx.	4, 5	2	0	22	46	2
Morus rubra L.	4, 3	1	0	11	38	1
Viburnum prunifolium L.	4	1	0	7	38	1
Prunus serotina Ehrh.	4, 3	1	0	5	23	1
Shrub layer:						
Hydrangea arborescens	3, 2	3	1	53	70	4
Rubus spp.	3, 2	2	0	39	92	3
Rhus toxicodendron L. and var. *radicans* (L.) Torr.	2, 3	2	0	39	77	2
Sassafras albidum	3, 2	2	0	24	62	2
Azalea nudiflora	3	2	0	31	54	2
Ceanothus americanus	2, 3	1	0	18	62	1
Kalmia latifolia	3, 2	1	0	19	46	1
Vaccinium vacillans Kalm	2, 3	2	0	22	38	1
Chionanthus virginica L.	3, 4	1	0	11	31	1
Polycodium stamineum	3	1	0	6	31	1
Viburnum acerifolium L.	3	1	0	8	23	1
Alnus rugosa (Ehrh.) Spreng.	3	1	0	4	15	1
Rhus copallina	3	1	0	4	15	1
Hamamelis virginiana	3	1	0	5	8	1
Epigaea repens	1	1	0	1	8	1
Woody vines:						
Vitis spp.	4, 1, 3, 5	3	1	80	100	5
Parthenocissus quinquefolia (L.) Planch.	1, 3, 4	3	1	67	100	4
Smilax spp.	2, 4, 3	2	0	24	62	2
Tecoma radicans (L.) Juss.	3, 2, 4	1	0	6	23	1

TABLE 3 (*Continued*)

Species	S	A	C	F	P	Co
Herbs:						
Cimicifuga racemosa (L.) Nutt.	2	3	1	67	100	4
Leguminosae spp.	2	3	0	65	100	4
Galium spp.	2	3	0	58	100	4
Polystichum acrostichoides	2	3	1	65	85	4
Panicum spp.	2	2	0	50	92	3
Viola spp.	2	2	0	49	92	3
Arisaema triphyllum (L.) Schott	2	3	1	57	85	3
Compositae spp.	2	2	1	48	85	3
Heuchera spp.	2	2	0	39	85	3
Smilacina racemosa	2	2	0	51	77	3
Asplenium platyneuron	2	2	0	36	92	2
Trillium catesbaei Ell.	2	2	0	32	92	2
Chimaphila maculata	2	2	0	39	85	2
Botrychium virginianum (L.) Sw.	2	2	0	31	85	2
Solidago spp.	2	2	0	34	77	2
Euphorbia corollata	2	2	0	29	77	2
Coreopsis major	2	1	0	21	77	2
Sanguinaria canadensis L.	2	2	1	30	62	2
Uvularia perfoliata L. and *U. sessilifolia* L.	2	2	0	28	62	2
Dioscorea glauca	2	2	0	25	62	2
Circaea latifolia Hill	2	2	0	24	62	2
Sanicula canadensis L.	2	1	0	24	62	2
Adiantum pedatum L.	2	2	0	23	62	2
Andropogon spp.	2	2	0	23	54	2
Athyrium asplenioides	2	2	0	20	70	1
Pteridium aquilinum, 2 var.	2	1	0	17	54	1
Hieracium venosum	2	1	0	15	54	1
Gramineae spp.	2	1	0	14	54	1
Bromus purgans L.	2	2	0	23	46	1
Impatiens biflora Walt.	2	2	0	16	46	1
Houstonia tenuifolia	2	1	0	14	46	1
Agrimonia spp.	2	1	0	12	46	1
Phryma leptostachya L.	2	1	0	11	46	1
Aruncus dioicus (Walt.) Fernald	2	1	0	9	38	1
Antennaria spp.	2	1	0	12	31	1
Silene virginica L.	2	1	0	7	31	1
Thalictrum revolutum DC.	2	1	0	7	31	1
Phytolacca americana L.	2	1	0	5	31	1
Osmunda cinnamomea	2	1	0	10	23	1
Anemone virginiana L.	2	1	0	9	23	1
Erigeron ramosus (Walt.) BSP.	2	1	0	9	23	1
Scutellaria ovalifolia Pers.	2	1	0	9	23	1
Ambrosia elatior L.	2	1	0	7	23	1
Aureolaria spp.	2	1	0	7	23	1
Chrysopsis graminifolia var. *asper*	2	1	0	7	23	1
Dryopteris hexagonoptera (Michx.) C. Chr.	2	1	0	7	23	1
Iris verna	2	1	0	6	23	1
Woodsia obtusa (Spreng.) Torr.	2	1	0	6	23	1

TABLE 3 (*Continued*)

Species	S	A	C	F	P	Co
Oxalis europaea Jordan var. *bushii* Small	2	1	0	5	23	1
Steironema intermedium	2	1	0	5	23	1
Athyrium thelypteroides (Michx.) Desv.	2	1	0	8	15	1
Podophyllum peltatum L.	2	1	0	7	15	1
Hypoxis hirsuta	2	1	0	6	15	1
Silphium compositum	2	1	0	5	15	1
Pycnanthemum sp.	2	1	0	4	15	1
Carex sp.	2	1	0	3	15	1
Gillenia trifoliata	2	1	0	3	15	1
Goodyera pubescens	2	1	0	3	15	1
Hypericum sp.	2	1	0	3	15	1
Lilium carolinianum Michx.	2	1	0	3	15	1
Lobelia spicata Lam.	2	1	0	3	15	1
Deschampsia flexuosa	2	1	0	3	8	1
Fragaria virginiana Duchesne	2	1	0	3	8	1
Oenothera fruticosa L.	2	1	0	3	8	1
Polypodium polypodioides (L.) Hitchc.	2	1	0	3	8	1
Saxifraga virginiensis Michx.	2	1	0	3	8	1

NOTE: The following species occurred in only one site and therefore have a constancy of two per cent and presence of eight per cent: *Asarum* sp., *Asclepias tuberosa* L., *Ascyrum hypericoides* L., *Baptisia tinctoria*, *Benzoin aestivale* (L.) Nees, *Betula nigra* L., *Clematis* sp., *Dennstaedtia punctilobula* (Michx.) Moore, *Dryopteris marginalis* (L.) A. Gray, *Elephantopus tomentosus* L., *Eupatorium album* L., *Geum virginianum* L., *Hypopitys americana*, *Ilex montana*, *Ipomoea* sp., *Juniperus virginiana* L., *Lyonia ligustrina*, *Luzula echinata* (Small) Hermann; *Phoradendron flavescens; Pinus strobus* L., *Plantago lanceolata* L., *Polygonatum biflorum*, *Polypodium virginianum*, *Prunus persica* (L.) Stokes, *Rumex obtusifolius* L., *Salix nigra* Marsh., *Schrankia angustata* T. and G., *Scleria triglomerata* Michx., *Taraxacum palustre* (Lyons) Lam. and DC. var. *vulgare* (Lam.) Fern., *Tephrosia virginiana*, *Verbascum thapsus* L.

simmon are rather evenly distributed. On the east and north, red bud is more often found in ravines, while on the south it is more frequent on the slopes.

Except for transgressives and woody vines, the shrub layer is not well developed. Chestnut oak seems to be the most abundant tree species among both transgressives and seedlings. The other oaks and the hickories are also abundant in these strata, and seedlings of all the important hardwoods are present. It is the woody vines, however, that give the community its greatest unity. Grape and Virginia creeper are almost never seen outside the borders of the oak-hickory forest; but within it the presence of one or the other, or both, is 93 per cent (57 of 61 stations).

The herb layer is especially rich and varied, herbs being fairly numerous even in the most rocky places. On the moist flats and in those ravines in which the litter is not too thick, this stratum accounts for more than 75 per cent of the cover. The most widely and evenly distributed species is *Cimicifuga racemosa*, which has a frequency of 67 per cent. *Arisaema triphyllum*,

Smilacina racemosa, *Galium* spp., and species of legumes are important in moister sites. Ferns are abundant except in the driest sites. Though *Polystichum acrostichoides* (frequency 65 per cent) is the most uniformly distributed fern, other species frequently occur and often form fairly large colonies. On Poplar Flat and at lower altitudes on the south-facing slopes, a few species of composites dominate the herbaceous layer. The most important of these are *Polymnia canadensis* L., *P. uvedalia* L., *Verbesina occidentalis* (L.) Walt., *Parthenium integrifolium* L., and *Helianthus atrorubens* L.

Mixed Forest. Although interrupted by fields, orchards, pastures, and sites from which fire wood is cut each year, the mixed forest found near the base of the mountain (fig. 1) is not entirely a product of these disturbances. It is therefore included as a community. The soil is very stony and contains little humus. The slope is gradual, with broad, rounded ridges that are dissected by winding ravines.

Data from 16 stations taken from 5 stands (table 4) show that six of the seven constants are found in the upperstory, dwarfed *Vaccinium vacillans* being the seventh (frequency 76 per cent). All other shrubs have frequencies of less than 50 per cent. Constants among the trees are *Quercus montana* (frequency 90 per cent), species of *Carya* (combined frequency 93 per cent), *Pinus virginiana* (frequency 89 per cent), *Quercus alba* (frequency 89 per cent), *Quercus velutina* (frequency 83 per cent), and *Robinia pseudo-acacia* (frequency 79 per cent). *Quercus montana* is the only species in this community with an abundance value of 5. *Nyssa sylvatica* and *Oxydendrum arboreum*, with frequencies of 70 per cent, and *Quercus marilandica* (frequency 56 per cent) are the only other trees of importance. A few herbs have relatively high frequencies (50 to 75 per cent), but all are so widely spaced that their coverage is always less than 1 per cent.

The physiognomy is typical of dry, wooded hillsides in the upper Piedmont and offers a decided contrast to the richer oak-hickory forest higher up the slopes. Except for a few pines in openings, most species in the understory are hardwoods. Seedlings are chiefly oaks and hickories.

Top of the Knob. About one acre of comparatively flat land is found on top of The Knob. This is covered with large, angular slabs of quartzite. In the almost flat central area, chestnut oak is clearly dominant, but near the edge of the cliff this species is replaced by pine. *Pinus pungens* is most abundant at the very margin, while *Pinus rigida* occurs a little farther from the rim. *Oxydendrum arboreum*, *Nyssa sylvatica*, *Acer rubrum*, *Quercus borealis* var. *maxima*, and *Robinia pseudo-acacia* are present in the understory.

The shrub layer of the central area is dominated by ericads. On the west and north is a heath thicket in which the most important species, in order of their decreasing abundance, are: *Pieris floribunda*, *Kalmia latifolia*, *Rhodo-*

TABLE 4

Data for Mixed Forest with Stratification (S), Abundance (A), Coverage (C), Frequency (F), Presence (P), and Constance (Co) for each species

Species	S	A	C	F	P	Co
Usually found in upperstory:						
Carya spp.	5, 4, 3	4	1	93	100	5
Quercus montana	5, 4, 3	5	1	90	100	5
Pinus virginiana	5, 4, 3	4	1	89	100	5
Quercus alba	5, 4, 3	4	1	89	100	5
Quercus velutina	5, 4	3	1	83	100	5
Robinia pseudo-acacia	5, 4, 3	3	0	79	100	5
Quercus marilandica	5, 4	3	1	56	60	4
Liriodendron tulipifera	5, 4	1	0	30	80	2
Pinus rigida	5	2	0	25	60	2
Pinus echinata	5, 4	2	0	20	60	1
Quercus borealis var. *maxima*	5, 4	2	0	17	60	1
Quercus stellata Wang.	5, 4	1	0	17	40	1
Quercus coccinea	5, 4	1	0	13	40	1
Usually found in understory:						
Nyssa sylvatica	4, 5, 3	4	1	71	100	4
Oxydendrum arboreum	4, 3, 5	3	1	70	100	4
Acer rubrum	4, 5	1	0	38	100	2
Diospyros virginiana	4, 3	1	0	31	60	2
Morus rubra	4	1	0	17	40	1
Cornus florida	4, 3	1	0	20	20	1
Shrub layer:						
Vaccinium vacillans	2, 3	3	1	76	80	5
Rhus toxicodendron	2, 3	2	0	49	80	3
Ceanothus americanus	2	2	0	35	60	3
Rubus spp.	3	2	0	40	80	2
Sassafras albidum	3, 4, 2	1	0	23	60	2
Rhus copallina	3	1	0	13	40	1
Kalmia latifolia	3	1	0	11	40	1
Hydrangea arborescens	2	1	0	13	20	1
Azalea nudiflora	3	2	0	4	20	1
Woody vines:						
Parthenocissus quinquefolia	5, 1	2	0	27	40	1
Vitis aestivalis Michx.	4, 1	1	0	18	40	1
Smilax rotundifolia	2	1	0	16	40	1
Herbs:						
Leguminosae spp.	2	3	0	73	100	4
Andropogon spp.	2	2	0	63	100	4
Panicum spp.	2	2	0	62	100	4
Solidago spp.	2	2	0	59	100	4
Hieracium venosum	2	2	0	43	60	3
Chrysopsis graminifolia var. *asper*	2	2	0	39	60	3
Houstonia tenuifolia	2	2	0	36	60	3
Chimaphila maculata	2	2	0	35	80	2
Tephrosia virginiana	2	2	0	28	60	2
Coreopsis major	2	1	0	24	60	2
Gramineae spp.	2	1	0	23	60	1
Compositae spp.	2	1	0	27	40	1

TABLE 4 (*Continued*)

Species	S	A	C	F	P	Co
Antennaria spp.	2	2	0	19	40	1
Pteridium aquilinum, 2 var.	2	1	0	13	40	1
Seriocarpus asteroides	2	1	0	13	40	1
Tripsacum dactyloides L.	2	1	0	20	20	1
Steironema intermedium	2	1	0	13	20	1

NOTE: Each of the following species occurred in only one station and therefore had a constance of six per cent and presence of twenty per cent: *Alnus rugosa, Amelanchier canadensis, Asclepias tuberosa, Aureolaria virginica* (L.), Farw., *Baptisia tinctoria, Castanea dentata, Cimicifuga racemosa, Dioscorea glauca, Euphorbia corollata, Fragaria virginiana, Fraxinus* sp., *Galium* sp., *Gaylussacia baccata, Gramineae* sp., *Heuchera americana* L., *Hypoxis hirsuta, Ilex opaca* Ait., *Juglans nigra, Plantago lanceolata, Polystichum acrostichoides, Potentilla* sp., *Rhododendron catawbiense, Schrankia angustata, Scleria triglomerata, Tecoma radicans, Viburnum prunifolium, Ulmus fulva, Prunus persica.*

dendron catawbiense, Smilax rotundifolia, and *Vaccinium corymbosum* var. *pallidum. Pieris* disappears along the east rim, being replaced by *Rhododendron catawbiense.* Here the thicket is tall and, in addition to the rhododendron and other species listed above, includes: *Leucothoe recurva, Gaylussacia baccata, Vaccinium vacillans,* and *Hamamelis virginiana.* Along the south rim the shrubs, chiefly huckleberries and laurel, are slightly less abundant. Herbs are scattered and of little importance except along the paths.

DISCUSSION

The Major Communities. Certain species are fairly abundant in all communities: namely, *Quercus montana, Nyssa sylvatica, Vaccinium vacillans, Oxydendrum arboreum,* and *Robinia pseudo-acacia.* Other species are present in all communities but in lesser numbers. These are, in order of their decreasing abundance: *Pinus rigida, Kalmia latifolia, Carya* spp., *Andropogon scoparius, Leguminosae* spp., *Azalea nudiflora, Solidago* spp., *Quercus borealis* var. *maxima, Sassafras albidum, Panicum* spp., *Chimaphila maculata, Chrysopsis graminifolia, Pteridium aquilinum, Hieracium venosum, Houstonia tenuifolia,* and *Tephrosia virginiana.*

The four major communities are thus related by a number of species common to all. At the same time, they differ in a number of respects, which were used as a basis of distinction. First, a comparison of their frequency diagrams (fig. 2) indicates certain differences in homogeneity. The oak-hickory forest has far more species but fewer constants than either of the other communities. As indicated by the diagram, it is the most heterogeneous of the communities. The chestnut oak—heath, with the fewest species, is the most homogeneous community. This results partly from the almost total absence of an herb stratum. Although the chestnut oak—black pine forest has the largest number of species with average frequencies exceeding 80 per cent, its heterogeneity is exceeded only by that of the oak-hickory forest.

Differences are further emphasized by the restriction of certain species to single communities. *Parthenocissus quinquefolia* and *Vitis aestivalis* are so widely distributed in the oak-hickory forest and so rare outside of it that they may almost be considered as its indicator species. *Juglans nigra*, *Fraxinus* spp., and *Cercis canadensis* are also limited to this community; as are certain woody species which are exclusive to the ravines: namely, *Ulmus fulva*, *Morus rubra*, *Viburnum prunifolium*, *Prunus serotina*, *Chionanthus virginica*, *Viburnum acerifolium*, *Alnus rugosa*, and *Tecoma radicans*. A

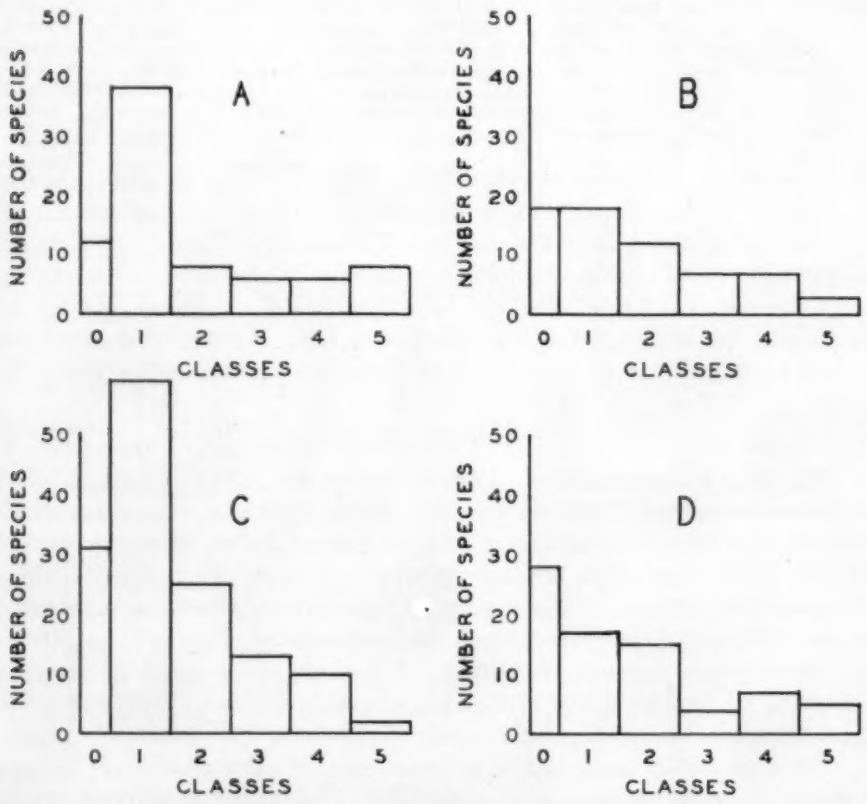

FIG. 2. Distribution of frequency classes in (A) chestnut oak—black pine, (B) chestnut oak—heath, (C) oak-hickory, and (D) mixed forest communities.

large number of mesophytic herbs, including most of the ferns, are limited to the oak-hickory forest. *Vaccinium corymbosum* var. *pallidum*, *Pieris floribunda*, and *Leucothoe recurva* are exclusive to the chestnut oak—heath, while *Rhododendron catawbiense*, *Galax aphylla*, and *Quercus ilicifolia* are rare outside of it.

Although the chestnut oak—black pine and chestnut oak—heath communities appear to be superficially similar, careful study reveals certain funda-

mental differences, because of which the two were treated as separate entities. In addition to differences already stated, there is a great variation in the stratification. In the chestnut oak—black pine community the understory trees constitute the densest stratum, while transgressives are very important in the shrub layer; in the chestnut oak—heath the shrub stratum is decidedly the most important layer, few transgressives are present, and the seedlings are almost entirely of shrub species. In the chestnut oak—black pine community herbs are scattered but always present; in the chestnut oak—heath they are practically lacking except in paths and openings. In the oak-pine community black pine has essentially the same sociological values as chestnut oak and is generally and uniformly distributed throughout the forest; in the oak-heath, however, the pine largely occurs in small colonies, while oak is the general dominant. Furthermore, blackjack oak is a constant in the oak-pine community but is rare in the oak-heath.

Relationships to Mountain and Piedmont Communities. Although now all removed, the original forest of the Piedmont was hardwood with some pine (Oosting 1942). The principal trees in the virgin forest of Surry County were white, red, post, and chestnut oaks, maple, hickory, sourwood, tulip poplar, and white and shortleaf pine, and second growth of the same species now covers about 60 per cent of the county (Davis and Goldston 1937). Strangely, chestnut is not mentioned. At present there are very few shortleaf pine and still fewer white pine in the vicinity of, or on, Pilot Mountain. Virginia pine is abundant, characteristically occurring in young, dense stands as it does elsewhere in the upper Piedmont. Older forests near the mountain are similar to the mixed forest around the base of The Pilot.

Ashe (1922) described a black pine—chestnut oak—scarlet oak association as a forest type of the Appalachians found, in general, on north- and west-facing slopes in middle altitudes but, near its southern limits, confined to sandy or gravelly soils on northwest slopes at higher altitudes. This almost exactly describes the small area on Pilot Mountain in which scarlet oak is important. For lower crests Ashe lists Virginia pine, chestnut oak, table mountain pine, scrub oak [*Quercus ilicifolia ?*], tulip poplar, and white hickory. All these species except tulip poplar occur on the summit of The Pilot, with black pine in addition. Ashe assigns chestnut oak to "stone-loving associations" and states that chestnut oak consociations are especially found on soils derived from sandstone and shale. The scrub oak he assigns to small areas in the mountains of Virginia, West Virginia, and Maryland, and northward on shallow soils derived from sandstone and shale.

Cain (1930, 1931) describes certain communities of the Great Smoky Mountains, which he calls subclimax pine-heaths and which are very similar to the chestnut oak—heath on The Pilot. He attributes the heath balds of the

Smokies to a postclimax condition after landslide, windfall, or fire on sites in which ericads were abundant prior to burning. He also states that *Kalmia latifolia, Rhododendron catawbiense,* and species of *Vaccinium* are particularly resistant to fire. The associations he considered were on sandstone, sandstone conglomerate, quartzite, or slate, all of which produce inorganically acid soils. Except for altitude, these conditions are duplicated on Pilot Mountain and are evidently responsible for the chestnut oak—heath, which, near the base of The Knob, approaches the structure of a heath bald.

Thus the chestnut oak—black pine and chestnut oak—heath communities are evidently more closely related to the vegetation of the mountains to the west than they are to that of the Piedmont. Although certain species of the oak-hickory forest are similar to those of the climax forest of the Piedmont as given by Oosting (1942), the importance of chestnut oak and the presence of certain herbs more common to the mountains than to the Piedmont indicate that this community is likewise related to the vegetation of the mountains. The fact that, except for the mixed forest of the base, the vegetation on Pilot Mountain is more closely related to that of the Appalachians than to that of the surrounding Piedmont may be partly explained by the obvious effect of altitude and partly by the rock formation and soil found on the mountain. Quartzite is uncommon in the Piedmont, and the Hartsells soil is similar to sandstone soils that are found in the southern Appalachians (Davis and Goldston 1937).

Habitat Factors. As to habitat factors that may control the distribution of the communities on Pilot Mountain, it is difficult to generalize. The chestnut oak—heath and and oak-hickory forest are usually present on steep slopes and flats; the chestnut oak—black pine community and mixed forest are found only on gently rounding slopes. Limitations in exposure and altitude have been pointed out in the descriptions of the communities. As to soils, the locations occupied by oak-hickory forest seem richest in humus. The north ravine down which the chestnut oak—heath extends and the ridges on either side comprise the single restricted area of Hanceville soil. The western half of the mountain seems more rocky than the eastern half, and the areas occupied by oak-hickory forest are, in general, less rocky than those above and below. The prevailing wind is from the southwest, and therefore the east- and north-facing slopes offer the most protected sites. Most of the rain clouds also come from the southwest, but, probably because of the contour of the mountain, there appears to be more precipitation on the northeast slopes than elsewhere. Thus a combination of factors restricts the most favorable sites to the northeast and north slopes east of Grindstone Ridge. The areas on the southeast and south that are occupied by oak-hickory forest appear to offer the next best conditions. Those occupied by the chestnut oak—black pine community are, in general, relatively xeric. The least

favorable of all sites are those around the base that are occupied by the mixed forest.

Disturbance. In addition to these continuously operating factors, a number of disturbances have influenced the extent and character of the vegetation. Rock slides locally destroyed the plants in their paths; the chestnut was removed by blight and fire; lumbering activities were extensive throughout the lower altitudes; and much of the area in the lower altitudes was formerly cleared. The influence of all these factors is, however, dwarfed by that of fire. The frequent burnings, which persisted until the building of the toll road, probably eliminated several species, while favoring the increase of those that were able to reproduce by sucker sprouts.

Succession and Modifying Factors. The oak-hickory forest is reproducing itself without any noticeable change, as is indicated by the frequent recurrence of its dominant species in the understory, transgressive, and seedling strata. It is therefore a climax community in which chestnut oak is the most important single species; tulip poplar forms societies of varying size; and northern red oak, white oak, several hickories, and black locust are important associates. In parts of the mixed forest that have not been recently disturbed the abundant hardwoods of the lesser strata indicate that this community is successional to the oak-hickory climax.

Generalizations on the dynamics of the chestnut oak—black pine community are complicated by the constant presence of pines in both understory and transgressive strata. The community is probably preclimax to the oak-hickory association, being controlled by the xeric conditions imposed by the thin, rocky soil. Although chestnut oak and blackjack oak may increase in importance, pine will probably remain abundant indefinitely because of the numerous openings in which it may grow to maturity. The extreme rockiness of the surface and the thin veneer of soil lessen the chances that the canopy may become closed. The small area in which scarlet oak is dominant is obviously a variant of the oak-hickory climax. Since pines are present in all strata, it has evidently not yet reached a climax condition. The chestnut oak—heath may be considered as a subclimax which is the result of repeated fires. Since seedlings of tree species are almost completely absent but shrubs are reproducing freely, the ericads will probably retain their present importance for some time.

A sawmill has recently been placed in the vicinity of The Pilot, and logs may be cut on the mountain itself. Such activities in the mixed forest should favor its retention in the present state. An increasing demand for lumber may cause the cutting of many of the trees in the oak-hickory forest, especially in lower altitudes. Whether such activities will result in an upward extension of the mixed forest remains to be seen. Because of their poor quality, it is doubtful that many trees in the chestnut oak—black pine com-

munity will be cut except for fuel. The unsatisfactory agricultural usefulness of the mountain has been amply demonstrated in the past. It is unlikely that any extensive clearing for cultivation will be attempted again, although the loam soils and the increased rainfall near the mountain will remain tempting to farmers.

The effects of all these possibilities are minor when compared to what might result if fire wardens relax their watch, a not improbable happening under present conditions. Should serious fires occur, chestnut oak, blackjack oak, red maple, and those shrubs which, like the trees named, come up from sprouts after fire, could increase in importance. Pines, however, might be temporarily increased since, under similar conditions in the Piedmont, pines have been found to appear and to grow so rapidly that a mixed forest resulted (Oosting 1943). Laurel and related ericads are now important in the moister sites within the chestnut oak—black pine community, and fire might cause the physiognomy here to become more like that of the chestnut oak—heath. The generally dry conditions of the area, however, are unfavorable to laurel, and the community, as a whole, would likely return to something similar to that of the present. Previous fires are said to have reduced the number of pines in areas now occupied by the chestnut oak—heath, and fire might conceivably bring this community nearer to a true heath bald. All species now present on the mountain have survived numerous fires and probably none would entirely disappear because of another burning.

SUMMARY

1. A phytosociological survey of the vegetation on Pilot Mountain was made during the summers of 1941 and 1942.

2. The Pilot is located in the southeastern corner of Surry County, North Carolina, and is the most southwestern outpost of the Sauratown Mountains. It rises nearly 1500 feet above the gently rolling plateau of the upper Piedmont to an altitude of 2413 feet. Quartzite caps the mountain. The soil is chiefly Hartsells stony fine sandy loam and is derived from the underlying quartzite, a rock formation that is uncommon in the Piedmont. Lumbering, cultivation, disease, and insects have affected the vegetation, but the greatest disturbing influence has been that of fire.

3. A statistical study was based on 158 sample areas, which were spaced altitudinally along "transects" ascending nine slopes and eight ravines. The data are summarized for each of the four major communities: chestnut oak—black pine, chestnut oak—heath, oak-hickory, and mixed forest.

4. The chestnut oak—black pine community covers the western half of the mountain and the higher southern slopes. *Quercus montana* and *Pinus rigida* are the dominant species. Important associates are *Quercus marilandica, Oxydendrum arboreum, Nyssa sylvatica, Vaccinium vacillans,*

Kalmia latifolia, and species of *Andropogon*. The community is probably preclimax to the oak-hickory association, being controlled by the xeric conditions imposed by the thin, rocky soil.

5. The chestnut oak—heath is found on the higher north and east-facing slopes. Locally its structure approaches that of a true heath bald. Chestnut oak and small colonies of pines are found in a widely scattered upperstory above a dense thicket in which ericads predominate. The community is very similar to the pine-heaths of the southern Appalachians and may be considered as a chestnut oak subclimax which is the result of repeated fires.

6. The mesophytic oak-hickory forest is a climax community found in the ravines and on the middle slopes of the eastern half of the mountain, *Quercus montana*, *Q. borealis* var. *maxima*, *Q. alba*, *Carya* spp., *Robinia pseudo-acacia*, *Liriodendron tulipifera*, *Vitis aestivalis*, *Parthenocissus quinquefolia* and a variety of herbs are important.

7. The mixed forest is found around the base of the eastern half of the mountain. *Quercus montana*, *Pinus virginiana*, *Q. alba*, *Q. velutina*, *Robinia pseudo-acacia*, *Nyssa sylvatica*, *Oxydendrum arboreum*, and *Q. marilandica* are the most important tree species. The mixed forest is a late successional community which, if left undisturbed, should rapidly approach the oak-hickory climax.

8. The mixed forest of the lower slopes is the only community definitely related to the vegetation of the upper Piedmont. All other communities show definite affinities to those of the southern Appalachians. This is probably related to similarities in soil and rock formation.

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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 71, No. 1, pp. 46–76 JANUARY, 1944

SUBCLIMAX PRAIRIE[1]

A. L. McCOMB AND W. E. LOOMIS[2]

The causes for the formation and persistence of the prairie peninsula which covers Iowa, southern Minnesota, and Wisconsin, and northern Missouri, Illinois, and Indiana, have formed the basis for much controversial speculation. The prairies from central Iowa eastward were classed as subclimax in the first edition of Weaver and Clements (43), but are shifted to climax in the second edition (1938), in which the entire peninsula is classed as a climax formation. This shift is in line with the stands of Shimek (32) and Transeau (38), but ignores much evidence that oak-hickory communities are capable of establishing and maintaining themselves on the most exposed sites and on most of the soils of Iowa, even though their rate of spread at many points may have seemed insignificantly slow.

Gleason (12) has summarized the taxonomic and earlier geological evidence for the establishment of the prairie peninsula in a post-glacial, xerothermic period of relatively recent date. Gleason cites invasion of the Illinois prairie, since grass fires have been controlled, at a rate which he considers proof of a forest climate at the present time. Aikman (1) found forest spreading in eastern Nebraska although he considered it to be a postclimax associes. Sears (30, 31) has published a number of papers on pollen analyses from the eastern end of the prairie peninsula indicating a gradual rise in temperature during post-Wisconsin time with one or more dry or xerothermic intervals, although pleistocene climate, except during glacial intervals, does not appear to have varied greatly from its present level. Simonson (33) has found buried soil profiles in Iowa which indicate that both soil-forming conditions and vegetation during the Sangamon inter-glacial period were similar to those that have prevailed during Peorian and recent times. Planosol profiles comparable to those currently present under grass (Putnam) or under forest (Marion), and gray-brown podzolic profiles comparable to the present Lindley (forest slopes), are found in Kansan till under 3–12 feet of Peorian loess. The distribution of these profiles indicates that the vegetation of Iowa during the Sangamon period differed from that at the time of settlement mainly in showing more forest in the western part of the State. Dissected valley slopes were covered by forest and the level till plain by prairie; with forest spreading onto the plain from the dissected areas.

[1] Journal paper No. J-1134 of the Iowa Agricultural Experiment Station, Project No. 612. Publication assisted by the publishing fund of Iowa State College.

[2] The authors are indebted to Drs. R. W. Simonson and P. H. Carr for assistance with soil profile studies and aerial surveys respectively.

Lane (20) has shown by pollen analyses that prairies were prominent in Iowa in the interval between the Nebraskan and Kansan glaciations, but that coniferous forests both followed and preceded the various glacial periods. He notes that in neither the Aftonian nor the Sangamon inter-glacial periods did he find evidence of persistent hardwood forests. His findings thus do not support a recent origin for the prairie. Another paper by Lane (19) contains pollen analyses from a peat bog in Hancock County in north central Iowa which are significant as indicators of climatic conditions during the last few thousand years. Observations on a 15-foot peat section showed that at least the immediately surrounding areas of this late Wisconsin (Mankato) drift section have been covered successively by (a) spruce, (b) mixed coniferous forest, (c) hardwood forest or savanna, and (d) grass, since the recession of the Wisconsin lobe which covered north central Iowa. Grass pollen first became prominent (14 per cent) in the 11th foot at the time of the shift from coniferous to deciduous forest species, and was dominant (60 per cent) in the 7th foot of the deposit. Weed pollens suggestive of recently bared areas, possibly of intermittent drying of the lake, accompanied the disappearance of the oak in the 8th foot, and reappeared in the 5th, 4th, and 3rd feet. There seems to be no doubt that all of the peat studied had been formed since the recession of the Wisconsin lobe some 20,000 years ago. We may assume that peat accumulated slowly at first in the deeper lake and that the lower 6 feet, in which various tree pollens were dominant, cover more than half, possibly more than two-thirds of post-Wisconsin time. We may assume also that with the filling of the lake and lowering of the outlet, peat deposition was accelerated until it may have approached a rate of one foot in 100 or 200 years. Lane's bog lay within a belt of low morainal hills which should have been better adapted to forest than the glacial till plain. We cannot assume therefore without further analyses that all or even most of Iowa has been forested in post-Wisconsin time. His data, however, seem to show clearly that the climate of Iowa has become warmer and drier during this period, and that the vegetation of the state has been subjected to unusual drought stress on two occasions, the first probably 5,000 to 8,000 years ago and the last possibly as recent as 500 to 1,000 years.

Lane's analyses, taken together, indicate that prairies have been prominent, if not dominant, in Iowa since the beginning of the pleistocene or glacial age, and he interprets them as supporting a climax classification for the prairie. The grassland community covered from 80 to 90 per cent of the state of Iowa at the time of white settlement, and was so thoroughly established on all but the rougher lands of the southern and eastern counties as to seem to justify a climax ranking. Transeau (38) has attempted to establish a tongue of prairie climate over the peninsula which would make it a true or climatic climax. Others (6, 7, 12) feel that the prairie peninsula,

including most of Iowa, is a relict of glacial disturbances maintained by soil factors, past xerothermic periods, and fires, and is therefore subclimax (to forest) or postclimax (to climax prairie) or disclimax (maintained by fire and soil factors), but in any event not true climax under present conditions.

Our justification for adding to the already voluminous literature of the prairie peninsula is based upon: (a) additional evidence of the recent rapid and general advance of forests in the critical western counties of Iowa; (b) observations upon the effects of the 1930–1939 dry cycle on Iowa forests; (c) soil studies which bear upon the problem of the advance of the forest; and (d) evidence for previously unrecognized soil factors retarding afforestation of the prairies of Iowa. While our observations are principally on Iowa, as the exposed, western base of the prairie peninsula, the discussion is extended to include similar grasslands wherever found. To forestall possible disagreements over terminology, we do not include soil factors, with their continuous changes from weathering and reaction, in our definition of true or climatic climax.

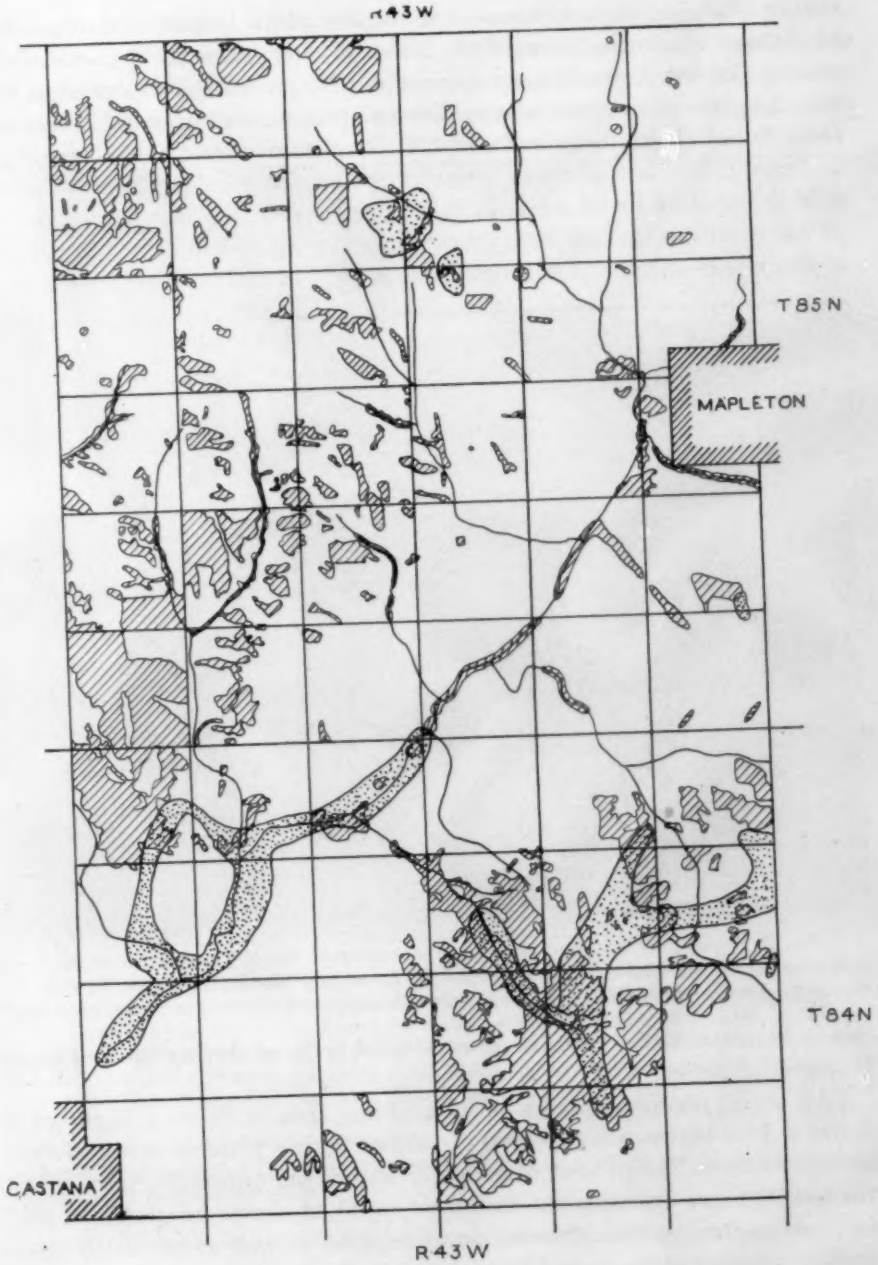
RECENT AFFORESTATION IN IOWA

A plant community which occupies more than 90 per cent of an area would normally be assumed to be the climax formation, and notes of the original surveyors show that many west central Iowa counties were almost treeless. If we assume a recent climatic shift, however, and the evidence for such a shift is unmistakable, the climax formation would be identified by its current invasion and ecesis rather than its distribution. On this basis, the loess hills of western Iowa, surprisingly, show striking evidence of recent rapid invasion by forest. Harrison, Monona, and Woodbury counties, on the Missouri river in central western Iowa, lie at the western edge and near the most exposed and the driest portion of the prairie peninsula. Harrison county vegetation was used by Shimek (32) to support his thesis of climax prairie in Iowa, yet 30 years later *Quercus macrocarpa* is spreading so rapidly on the less intensively farmed lands of the county as to constitute a serious economic problem.

Direct evidence of current afforestation in these critical western Iowa counties is furnished by two maps contrasted in figure 1. The distribution of the original forest, as mapped section by section in 1853 by the original public land surveyors, is shown along with the present forest cover mapped from aerial photographs taken for the Agricultural Adjustment Administra-

Explanation of figure 1

FIG. 1. Forested areas in Maple (85 N.) and a part of Center (84 N.) Townships in Monona County, Iowa. Dotted areas show closed forest of 1853, before settlement, and cross-hatched areas represent present forest distribution. Compare figure 2 which shows some of the west central portion of this area.


R43W
T85N
MAPLETON
T84N
CASTANA
R43W

tion in 1940. The maps cover most of two townships located in the loess hills of Monona county just east of the Missouri river bottoms. The soils of this area are of the Knox-Monona association. No podzolized soil profiles have been mapped in extreme western Iowa although small areas of forest soils recently have been discovered about 30–50 miles southeast of the area shown in figure 1. The lack of forest podzolization in this region indicates that the establishment of forest areas in this "prairie climax" was recent in time, probably within the last 1000 years, as well as limited in extent at the time of settlement of the region. Buried soil profiles in this region (33) show evi-

FIG. 2. Aerial photograph of the southwest corner of Maple Township showing 50 per cent or more of this original prairie covered by forest and woodland pasture. In 1853 "A few small groves—with a few scattering burr oak comprised the timber of the township."

dence, however, of the presence of considerable forest during the Sangamon interglacial period.

An aerial photograph of a portion of the area in figure 1 is shown in figure 2. This region was surveyed in 1853 as prairie with scattering trees or clumps of trees. The present forest cover has spread naturally, most of it in the last 50 years. Invasion has been most rapid, of course, in protected sites, but has resulted in the afforestation of exposed as well as protected slopes and of rounded ridge tops. The narrow, hogback ridges, which were once classed in a separate soil series, resist invasion even on northeast exposures and when partially shaded by well developed forest. Local soil factors would

appear to be involved. Most of the trees shown in the figure are *Quercus macrocarpa*, and only a few of them are more than 50 years old. Brush lands are in part reproduction from stumps and in part new invasion which is still proceeding. Most of this timber is, as shown in figures 3 and 4, rather scrubby

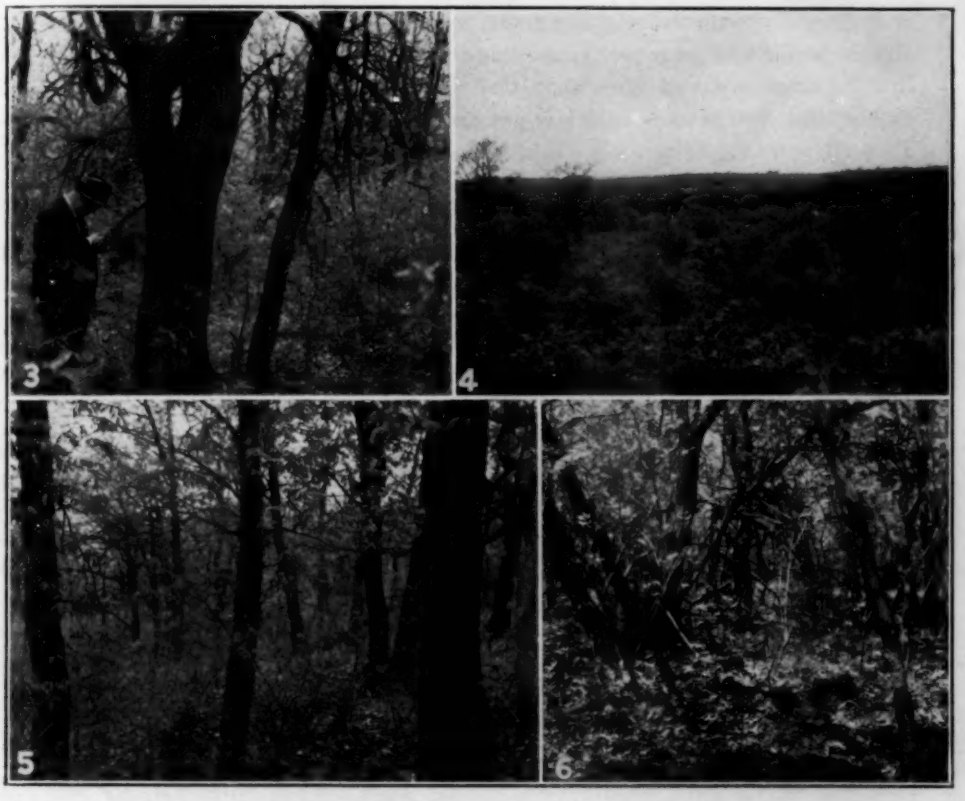


FIG. 3. A low-branched, 78-year old seed tree of *Quercus macrocarpa* surrounded by 40–50 year old trees which have formed a closed canopy with an understory of *Cornus*. Fully exposed ridge top in the center of section 31, Maple Township. FIG. 4. *Quercus borealis* and *Q. macrocarpa*, closed forest and cutover pasture. Looking southeast across section 10, township 86 north, range 43 west; Woodbury County just north of Maple Township in Monona County (*cf.* Fig. 1). FIG. 5. *Quercus borealis* closed forest with typical forest undergrowth on southwest slope in section 15 of township 86 N. Oldest trees about 50 years. FIG. 6. Seedlings of *Ulmus americana* and sprouts of *Quercus macrocarpa* on hilltop land in section 15, Maple Township. The elm apparently seeded into over-grazed pasture early in the 1930–39 dry cycle.

burr oak. The stands are closing or closed, however, until prairie species have been largely excluded and other forest species are now appearing. *Quercus borealis* (fig. 5) is capable of maintaining full stands on the most exposed sites, and is spreading into the burr oak, along with *Carya cordiformis*, as

seed trees develop. *Ulmus americana* is common, invading disturbed areas rapidly (fig. 6) and persisting as dominant trees even on the most exposed areas. *Tilia americana* grows vigorously on protected north slopes. *Juglans nigra, Gymnocladus dioica, Celtis occidentalis,* and others are found as scattered individuals, typically in more protected locations. *Fraxinus lanceolata* is moderately common, and the usual willows, maples and elms occupy the stream banks and younger flood plains.

The large areas of pure stands of burr oak, the prominence of *Cornus* rather than *Ostrya* as an understory, and the absence of old trees or stumps all testify to the recent establishment of these woodlands. The frequency with which the larger trees on many sites showed ring counts of 45 to 50 years suggests that a general climatic or economic disturbance, such as drought and over-grazing or abandonment of marginal farms, during the 1890's, may have accelerated the current invasion. Acceleration of invasion of grasslands by grazing is a common observation in the West and Southwest (9, 21). If forest was already invading slowly and the new community is able to develop vigorous stands on exposed sites, climax relationships are not involved, and the effect of the disturbance is considered to have been accelerative only.

Adequate evidence that the current trends antedate the disturbances which have hastened them is contained in notes made by the original surveyors and preserved in the State House at Des Moines. Excerpts from these notes for several townships in Monona and Woodbury counties, all of which were mapped in 1853, follow:

Twn. 83 N., R. 43 W., 5th P.M. David J. Sales, Deputy Surveyor. "Young timber is evidently extending into the prairie, and in many places there is a growth of young burr oaks, lind and hickory on high ground where there is no water course. We found no inhabitants or improvements in this Township."

Twn. 84 N., R. 43 W., 5th P.M. (*cf.* fig. 1), David J. Sales, Deputy Surveyor. "This Township (excepting the river bottom) is generally rolling, with some young timber scattered over it, generally burr oak and lind and numerous small thickets of young burr oak, lind and hazel which are evidently spreading in despite the fires which burn off the grass."

Twn. 85 N., R. 43 W., 5th P.M. (*cf.* figs. 1–3, 6, 13 and 14), John W. Ross, Deputy Surveyor. "The greater proportion of the Township is high rolling prairie. Soil 3rd rate. . . . A few small groves of timber principally maple lynn and elm with a few scattering burr oak comprise the timber of the Township."

Twn. 88 N., R. 43 W., 5th P.M., John W. Ross, Deputy Surveyor. "The Soil of which is poor 3rd rate. In the prairie are burr oak scattered all over."

From these notes and others not quoted we get the impression that the surveyors mapped as forest all tree-covered areas with a closed canopy, from

which the prairie grasses had been excluded either by trees or by trees and associated shrubs. The areas mapped as prairie thus probably consisted of both true prairie and burr oak savanna. In reading through notes for individual sections, quarter corners and section corners in areas mapped and spoken of as prairie were often witnessed by burr oak trees. These witness trees were frequently 200 to 300 feet from the section corners, indicating an open savanna, while their descriptions indicate young trees. In these localities at the present time there are areas of apparently lightly grazed original prairie in which are a few scattered burr oak trees. These areas of savanna are probably very much like areas found at the time of the survey.

In the 80 years since the area was first settled most of the original timber has been cut or cleared, and it is now difficult to locate any of the forest plotted in 1853. On the other hand the forest has invaded so generally and in such a wide variety of new sites as to leave little doubt that the climate at this extreme western end of the prairie peninsula is fully capable of supporting an oak-hickory climax. Invasion has followed land use patterns rather than topography, and recently forested spots are on rough, poor, and inaccessible land rather than in protected stream valleys. Much of the heaviest invasion appears to have been on foreclosed lands which have lain fallow or only partially utilized. Both new invasion and older stands may be found on hilltops and on south and west slopes (figs. 2–6), indicating that these forests require no protection from wind and sun. It should be noted, however, in connection with later discussions that these soils are formed from a deep, well-aerated loess subject to more rapid erosion than is characteristic of most of the prairie peninsula; also that surface and internal drainage are excellent and the soil nitrogen content low.

FOREST INVASION IN CENTRAL IOWA

Invasion in western Iowa has been favored by less intensive land utilization, by the rather general distribution of seed trees, and, as we shall note later, by soil conditions suitable for forest growth. On the Wisconsin drift soils of central and north central Iowa conditions have been less favorable for forest. Planted trees grow well throughout the region, however, and seedlings become established readily wherever the sod has been broken up (figs. 7, 8). In contrast an undisturbed *Poa pratensis* sod may delay invasion for years (fig. 9), and the rank growth of the original prairie was undoubtedly an inhospitable site for forest seedlings. Under these conditions primary invasion occurred along the streams where erosion had broken up the sod (figs. 11, 12, 21), and invasion of the till plain occurred in the usual shrub ecotone rather than by the widely scattered seed trees which have been the basis of the rapid afforestation in western Iowa. Current invasion is limited by intensive land utilization, but adequate evidence of moderately rapid

presettlement invasion of the prairie is shown by surveyors' notes and soils maps.

The coarser, lighter-colored prairie soils of the Wisconsin drift area in Iowa are mapped as Clarion, the finer-textured, black soils of the poorly drained swales as Webster. Forest on eroded valley slopes has formed the

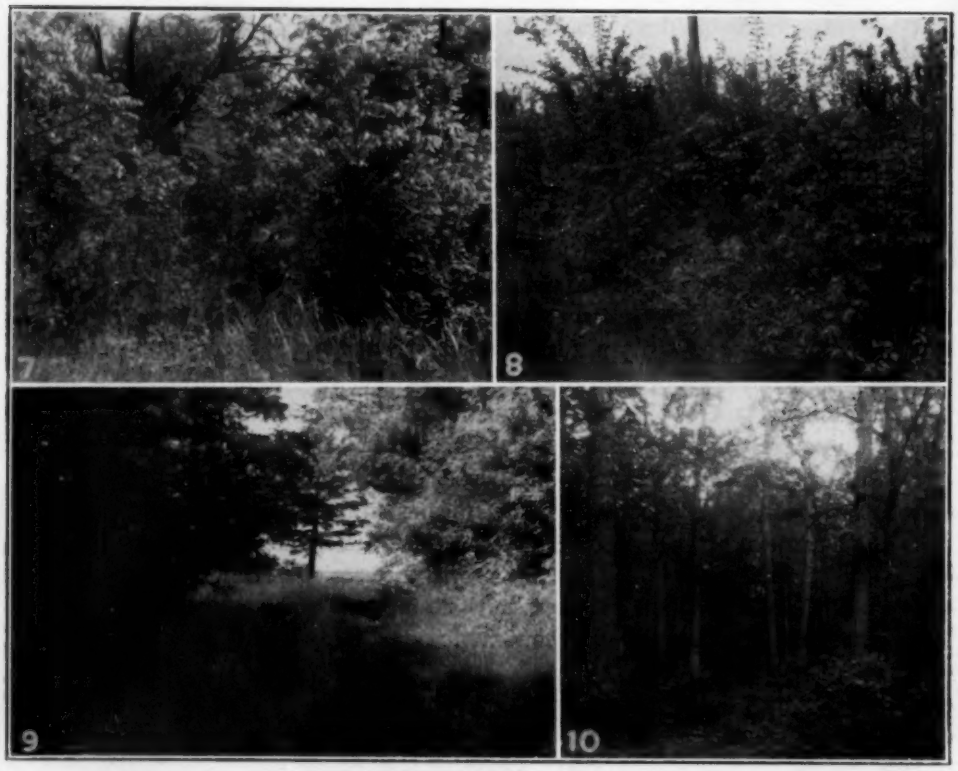


FIG. 7. Natural reproduction of *Juglans nigra, Acer saccharum, A. saccharinum, A. negundo, Fraxinus lanceolata, Celtis occidentalis,* and *Ulmus americana* in an abandoned kitchen garden. Prairie hilltop site; Clarion loam soil; Story County in central Iowa. FIG. 8. *Ulmus americana* seedlings on a road bank bared in grading operations three years previously. South exposure; no seepage from back. FIG. 9. The lawn of the same farmstead shown in figure 7. Undisturbed *Poa pratensis* sod has prevented the establishment of seedlings on this portion of the plot. FIG. 10. Second growth oak-hickory forest (*Quercus alba-Carya ovata*) on Wisconsin till (Ames soil type); Story County, Iowa.

Lindley, and on the till plain the Ames soils. Ames soils are formed from the same parent material as the Clarion, but under the more rapid podzolizing influence of the forest they have developed a gray, leached A_2- and a plastic B-horizon, to form inferior agricultural lands known as "oak lands" (figs. 10–12, 21).

Estimates of the time necessary for the formation of a planosol like the Ames or a gray-brown podzolic soil like Lindley are not available. Minimum estimates for the formation of podzols under spruce forests at more northerly latitudes are from 1000 to 1500 years (5). Under the climatic conditions of the western prairies and with a highly calcareous glacial till as parent material, a much longer period may be required for formation of mature soil profiles. The flat tops of several low Indian mounds on a forested divide near the Des Moines river in Boone county, Iowa, showed no visible evidence of

FIG. 11. Erosion and forest invasion along the Des Moines River, Boone County, Iowa. The oak-hickory forest has advanced along the deep gullies cut back from the glacial stream valley, and then spread over the prairies of the nearly level till plain. Scattered oaks in pastures and farmyards at the left and back are evidence that most of the area shown was originally covered with forest. (*Photo by P. H. Carr.*)

the development of a leached A_2-horizon, nor could any accumulation of clay to form a B-horizon be detected. These mounds are classed as woodland culture by Dr. C. R. Keyes, State Archaeologist, and are variously estimated to be from 1000 to 5000 years old. Undisturbed soils near the mounds showed a typical Ames profile with a heavy, plastic B-horizon. From this and other evidence it seems probable that from 1000 to 2000 years have been required in Iowa to produce detectable soil changes under forest, and that the fully developed Ames profile indicates a forest cover for considerably more than 2000 years.

Close examination of the soils of oak-hickory forests on the Wisconsin till plain shows that, with similar topography and drift material: (a) the outer border of the Ames soil is sharply demarcated; (b) there are often spots or bands of partially podzolized or degraded Clarion soil between the Ames and the Clarion; and (c) beyond the degraded Clarion an oak-hickory forest existed on typical Clarion prairie soil showing no visible evidences of podzolization or long occupance by forest. The sharp outer border of the Ames probably indicates a long pause in either invasion or retreat, for had conditions been uniformly favorable or unfavorable for forest the Ames would blend gradually with the Clarion. The presence of forest beyond the areas of Ames soil is undisputable evidence of a more recent invasion, probably one taking place in two steps, the first of which occurred long enough ago to permit partial podzolization of the invaded Clarion, and the second so recent as to leave no visible change upon the soil.

The distribution of Ames and Lindley soils bordering typical prairie streams in Story county, Iowa, along with the prairie-forest border mapped in 1847, are shown in figure 12 (*cf.* fig. 21). This map shows several items of interest: (a) The forest mapped along these prairie streams in 1847 exceeded the forest soils by more than four to one—clear cut evidence of a presettlement forest invasion so recent that no detectable soil profile changes had occurred. (b) The forest was advancing more rapidly along the streams than onto the till plain. (c) Eighty per cent of the forest soils are east of the streams and all of the Ames (till plain) soil is protected on the northwest by the streams, by steep banks or by marshes. In contrast, 40 per cent of the original forest lay west of the stream, most of it fully open to the northwest. Gleason (12) gives planimeter measurements of several Iowa maps showing that 70–80 per cent of the forest lay to the east of streams or lakes. He attributed this distribution to the firebreak action of the water. Fuller (10) records the same distribution of forest soils in LaSalle county, Illinois, and points out that low banked streams, or east-west streams, which would not have acted as firebreaks, showed no development of forest soils. It seems evident, however, that if fire was the major factor causing the unequal distribution in figure 12, the more recently established forests would have been affected as well as the older. In southern Iowa, where fires should have been equally prevalent, forest soils have been formed on slopes west and southwest of the streams—fully exposed to fire but protected from the drying effects of sun and wind. In addition to fire, this unequal distribution of forest soils on the Wisconsin drift may have been associated with the windbreak and afternoon shade protection afforded seedlings by the main forest body to the west, and by the fact that soils on the east sides of streams in Iowa and Illinois (34) often contain windblown sand and are somewhat lighter in texture.

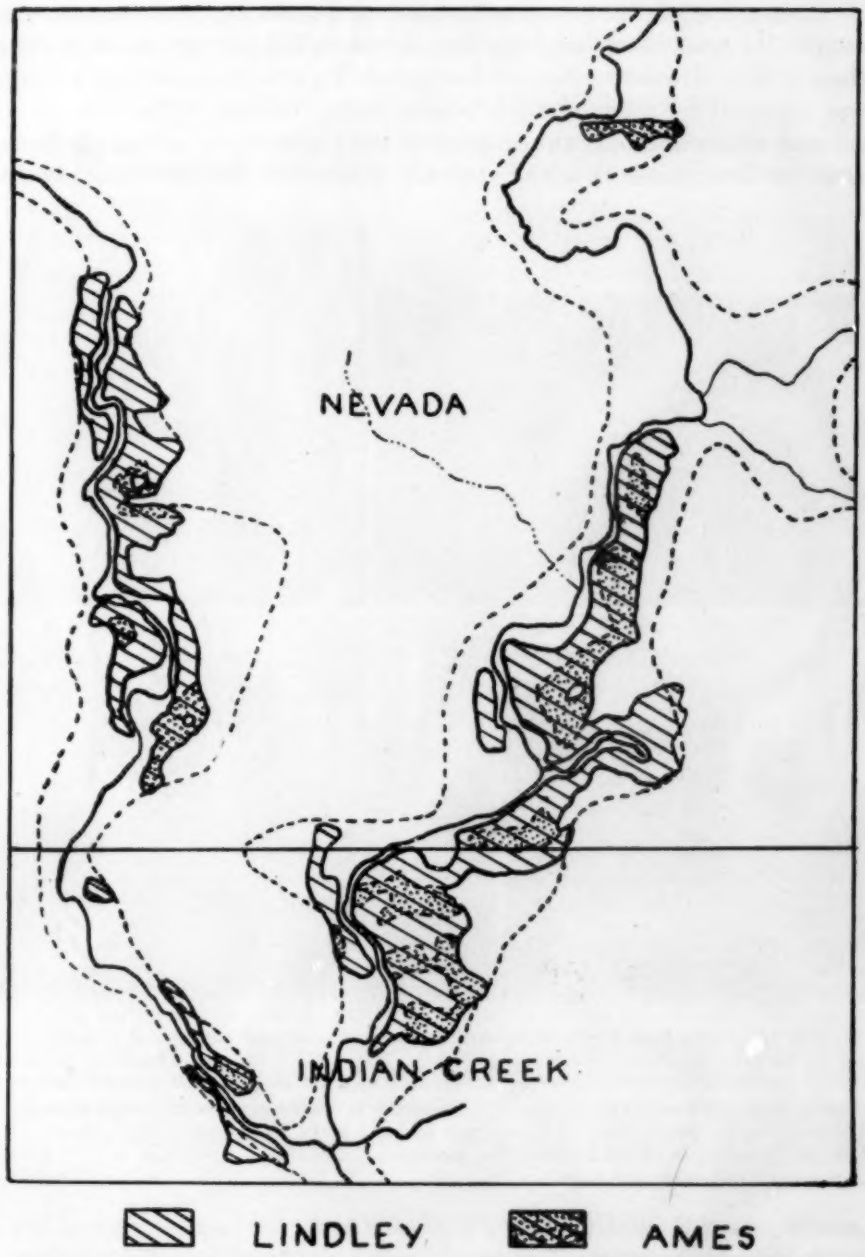


FIG. 12. Forests and forest soils in two Story County townships. In 1847 the streams were bordered by forest as shown by dotted line. Older forest had developed Lindley soils on valley slopes and Ames on the till plain. More than three-fourths of the forest had been established so recently that the original prairie soils were unaffected (*cf.* fig. 21).

Irrespective of the factors affecting distribution, the evidence seems to require the conclusion that forest has increased 300 per cent or more along these prairie streams in the last few hundred years, but that this advance was preceded by a considerably longer period during which little or no advance occurred. Abundant evidence of this recent forest advance is found along the Des Moines river and generally throughout the central and north-

FIG. 13. Young trees of *Quercus macrocarpa* in exposed and unpastured prairie showing no damage from drought. Monona County, May 1937. FIG. 14. Dominant trees of *Ulmus americana* dead and *Quercus macrocarpa* injured in protected pasture. Monona County, May 1937. (*cf.* figs. 3–6). FIG. 15. *Quercus macrocarpa* in over-grazed pasture with southwest exposure dead or killed back to main limbs. Woodbury County, May 1937. FIG. 16. No injury in mixed hardwood reproduction. One hundred yards east of area shown in figure 15 and same exposure.

eastern part of the state. On deep loess soils in the northeast corner of Iowa entire townships of prairie soil were covered by recently established forest. It is noteworthy, however, in connection with soil factors to be discussed later, that no comparable recent advance has occurred on the older soils of

the Kansan drift and associated loess in south central and southeast Iowa, an area which contained much of the state's original forest cover.

FOREST SURVIVAL DURING THE 1930–1939 DROUGHT

The years from 1930 to 1939 covered one of the most severe and protracted dry periods in the recorded history of the Mississippi valley. If the normal climate of Iowa is that of a grassland climax, forests should have suffered severely during this dry cycle. Paradoxically, although hundreds of thousands of adapted trees on suitable or even protected sites were killed or very severely damaged, *forests* were not visibly affected. Unpastured savanna of *Quercus macrocarpa* in original prairie showed no injury on a severely exposed site in Maple township, Monona county (fig. 13), but heavily pastured burr oak a few miles north in Woodbury county was killed or severely injured (fig. 15). *Ulmus americana* was killed and burr oak injured on a moderately pastured north slope (fig. 14), while no signs of injury were evident in unpastured reproduction on the south slope of the same hill (fig. 6). In general, pasture fences marked the difference between serious injury to complete killing and no injury whatever (figs. 15, 16). In many of the pastures no perennial grasses could be found in May 1937. Conditions were ideal for rapid invasion by tree seedlings, particularly where the farmers had been forced to dispose of stock for lack of feed, but older trees were injured in spite of reduced competition. The only factor that could be associated consistently with drought injury was trampling of the soil. Trampling would have reduced rainfall penetration, but evidence to be presented later suggests that reduced aeration was the more important factor. *Quercus macrocarpa* is deep-rooted on these loess soils (fig. 23). Trampling, particularly heavy stocking of the finer-textured soils in early spring, would reduce gas exchange rates and so limit depth of root penetration, rate of absorbing root production and efficiency of roots present.

The recent drought seems thus to have furnished a clue to forest invasion and survival as well as evidence that undisturbed forest formations are able to withstand one of the severest droughts on record, at the dry western edge of the prairie peninsula. This lack of drought injury, coupled with presettlement and continuing forest invasion, indicates that the current climate of western Iowa is not too xeric to support an oak-hickory climax, and thus relegates the grasslands of the prairie peninsula to a subclimax ranking.

FACTORS FAVORING SUBCLIMAX PRAIRIE

The establishment of oak-hickory forest as the climax formation of Iowa leaves unexplained the presence of tall grass or true prairie as the dominant vegetation, covering 80 per cent or more of the state at the time of settle-

ment. Past attempts at explaining prairies have stressed climate, biologic factors, fire and soil factors. Undoubtedly all of these are concerned in varying degree in the persistence of the prairie peninsula.

Climatic Factors. Although our observations have shown oak-hickory forest capable of spreading and maintaining itself on the most exposed sites of western Iowa and in some of the driest years of record, the climate of this region is clearly borderline between the forest and the grassland climax. The rainfall of about 30 inches falls predominantly during the growing season. The amount and rate of precipitation in individual storms are high enough, however, to permit the subsoil wetting necessary for a deciduous forest, and moist soil from the surface to the water table at some part of the year is characteristic if not universal. Such rainfall distribution, while favorable to grass, is not unfavorable to forest.

Rainfall-evaporation ratios have been used as one of the better indices of climate as it affects vegetation. Unfortunately very few evaporation measurements are available for the construction of such ratios. Weather Bureau records of evaporation for the seven months April to November are available for the last ten years at Ames in central Iowa, and for five years at Clarinda in the southwestern and Cherokee in the northwestern part of the state. The seven months rainfall-evaporation ratio at Ames for the years 1933–1942 was 0.50. The average for five dry years was 0.35 and for five years with normal or excessive rainfall, 0.65. For the nearly normal five-year period 1938–1942, the ratio of the *seven months* evaporation to the *twelve months* rainfall was 0.72 at Ames, 0.70 at Cherokee and 0.64 at Clarinda. While winter evaporation is low, available estimates indicate that its inclusion would have lowered these ratios by 5–10 per cent. It seems probable, therefore, that the current rainfall-evaporation ratio in western Iowa is about 0.60. In contrast, Transeau (37) set 1.00 as the ratio for continuous forest and 0.60 as the border between prairie and short-grass plains. His ratios were based on data of a single year and would seem to be too high. An annual evaporation rate that is 170 per cent of the precipitation, however, cannot be considered ideal for forest, and is an index of the stress against which forest invasion is occurring.

Evidences of the recent dry or warm-dry periods stressed by Gleason (12) are unmistakable in Lane's pollen analyses (19) and in the Wisconsin drift, forest soil–forest distributions. These data give a picture of the oak-hickory forest only recently resuming its advance after a long period of stagnation. The presence of degraded or partially podzolized Clarion soils indicates that recent invasion has occurred in two waves separated by a period relatively unfavorable for forest. A picture of the time involved in these sequences can be obtained from Lane's Hancock County peat (19).

Assuming that the weed stages represent dry periods when the lake was partially dried up, that the rate of filling with peat increased gradually from zero at the bottom to 1 foot in 200 years for the upper foot, and that peat deposition occurred over a period of 20,000 years, the first dry period, represented by a sharp drop in oak and increase of grass pollen in the 7th foot of the deposit, would have occurred at a minimum of about 3500 years ago and at the maximum possibly 8000 years ago. The more recent weed stage and dry cycle, shown from the 5th to the 3rd foot, would have occurred approximately 1000 years ago with a minimum estimate of 400 and a maximum of 2000 years. The estimates for the first dry cycle correspond with those of 2000 to 6000 B.C. given by Antevs (2, 3), and with the estimates of Brooks (4), based on many records indicative of a general dry cycle over at least the mid-latitudes of the northern hemisphere. The more recent general dry period is estimated by Brooks to have occurred between about 800 and 1600 years ago and to have ended about 1100 A.D.

As the climate of late-glacial and post-glacial time gradually became warmer, the spruce forest that followed the ice was replaced by oak-hickory forest on the coarser-textured soils. Although evidence is lacking, it is possible that the flat, poorly aerated till plain (fig. 21) went directly from spruce to grass. The first dry period may be assumed to have driven the forest back to the borders of the present fully developed forest soils; Ames on Wisconsin till, Clinton and Marion on Peorian loess overlying Kansan till, etc. This scheme allows 6000 to 8000 years for the formation of the Ames profile, and assumes that the interval between the two drier periods was still too dry for forest invasion until toward the end, when the advances represented by scattered strips of degraded Clarion were made. Six thousand years is probably above the minimum time for forest soil profile formation in Iowa, but there is no upper limit, and we feel that 2000 years is below the minimum under the conditions which have existed. No intervening period fits with the climatological data available from many sources.

We thus arrive at the conclusion that, except for a short period some 2000 or 3000 years ago, grass was the climax formation of Iowa from 3000 or 6000 B.C. to 1000 or 1200 A.D., and that the present forest climate has had only a few hundred years in which to affect the vegetation of the area. Lest our outline seem too assumptious, may we repeat that soil profile data, all available fossil pollen analyses, and the best estimates of past global climatic shifts are in agreement in supporting its essential points.

Biologic Factors. Even with a longer period than has been available for forest invasion, the difficulties of seed distribution and seedling establishment under grass competition could account for the lack of forests in central and western Iowa. Direct invasion without a shrub ecotone, such as is re-

quired for rapid spread of the forest, is complicated by the fact that few forest species are fitted to compete with a prairie vegetation. Invading tree seedlings must develop a long tap root the first growing season if they are to get below the zone of heavy moisture use by grass and survive summer droughts. They must also make enough shoot growth to emerge from the dense lower layer of the prairie and make food for continued growth, and they must be capable of withstanding relatively long periods of drought when the soil moisture level is at the wilting point and the air temperatures within the drying grass, which affords little shade but effectively stops cooling air currents, may be above the death point of many plants. The first two characteristics are met with only in the large-seeded species, and when one considers periodicity of seed years and the great abundance of rodents in the prairie, the difficulties of invasion and ecesis are evident. Most of the species of oak seedlings also require some shading and moderate temperatures (17). In southern Iowa reproduction of cut-over oak stands in almost exclusively from sprouts, and seedling reproduction is successful only when small openings are made in unpastured and unburned forest. In central Iowa oak reproduction in non-forest areas is so rare that the presence of oak trees in a farm lot or fence row is taken as evidence of original timber (fig. 11). When these growth requirements are matched against the characteristics of available species, *Quercus macrocarpa* is the only one obviously fitted for invasion, but its high seed weight tends to limit dispersion and invasion.

In addition to the evidence given above, Weaver and Kramer (44) and Aikman (1) report a considerable spreading of *Quercus macrocarpa* in eastern Nebraska since settlement, and Weaver and Kramer point out that the root habits of this species are especially well adapted to development on well drained and aerated soils (*cf.* fig. 23). In contrast to burr oak, *Ulmus americana* seeds widely and grows quickly under favorable conditions and is probably the primary invading forest species in central Iowa at the present time. *Ulmus,* however, will not invade vigorous sod, even that of *Poa pratensis,* and its spread depends upon suppression of sod by *Rhus* or other shrubs, or by erosion, grazing or cultivation (figs. 6, 22). Once established, the elm encourages the spread of other species which may be expected to become dominant on all but flood plain sites.

The prairie soils, both immature and mature, are characterized by a microflora that differs sharply from that of the forest soils. One of the authors has recently discussed certain aspects of this problem (22, 23), and shown that the absence of mycorrhizal fungi may prevent the growth of forest species on prairie soils (fig. 17). White (45) and others have reported similar results. Whatever may be the physiological action of mycorrhizae, the absence of their component fungi would delay forest invasion and render improbable the occasional long jumps that would make rapid invasion possible.

Norman and Moody (26) have shown that the organic matter of forest and prairie soils differs in quality as well as quantity, and that forest organic matter is more active and capable of reducing twice as much hypoiodite as that of the prairie. Forest soils students know well the differences between humus types in various forests, and Rayner (29) has suggested that certain types of organic matter decomposition and humus formation may produce substances toxic to trees and to mycorrhizal fungi. Recent work suggests strongly that the roots of conifers are dependent on growth substances secreted by certain fungi or upon certain products resulting from active organic matter decomposition by these fungi. In a continuation of the work of Rayner, Neilson-Jones (25) has obtained evidence that organic compounds toxic to conifers are formed in moorland soils. Conditions are too different to make these results directly applicable to the grasslands discussed here. The authors, however, feel that studies of differences in both the organic matter and microflora of grass and forest soils should be continued. Such studies may help to explain why forest planosols are reforested with relative ease whereas contiguous grassland planosols are invaded slowly, even where the grass is disturbed.

Fire as a Factor Favoring Subclimax Prairie. There can be little doubt that the recent widespread invasion of forest on the prairie, and of other woody plants into areas of grassland in western United States, has been due to changes following settlement. Where the sod has not been broken these disturbances are due mainly to grazing and the use or disuse of fire. The rapid recent spread of tree and woody species on the Edwards plateau in Texas (9) and the invasion of the pinon-juniper and ponderosa pine types into grassland in Arizona (21) are both ascribed to the stoppage of grass fires and to the reduction of grass competition by grazing. In most instances these two factors act together and it is difficult to disentangle the effects of one from the other. We are inclined to believe, however, that the rapid forest advance in western Iowa has been due chiefly to reduction in grass cover by grazing and plowing rather than to prevention of fires. This belief is supported by the surveyors' notes or oak spreading into the prairie in spite of fire, and by the exposed position of younger forests on the Wisconsin drift (fig. 12). Acceleration of invasion cited by Gleason (12) and others as due to fire control could equally well have been effected by intermittent overgrazing.

The role of fire in modifying the forest-prairie boundary prior to settlement is difficult to evaluate. The effects of fires on forests have been more extensively investigated than the effects of fire on grasses. Among those who have written on the prairie-forest relationship the opinion generally prevails that fire has been an important factor retarding forest development. How-

ever, from the literature one can gain evidence for any stand desired (14). The effects of fires would undoubtedly vary with their frequency and severity and would depend upon whether the tree species were of the sprouting or non-sprouting variety and how well insulated the inner bark and cambium were from the short but intense heat of the prairie fires. Transeau (38) expresses the following view: "Fires favor the persistence of prairie species in contrast to tree species. Prairies preceded prairie fires. Whenever one searches the historical literature describing the period of settlement one is impressed by the frequent widespread fires usually ascribed to the Indians. Fire as an ecological factor, seems to boil down to this: that in forest climates it retards development, and may result in scrub, but it does not result in prairie. In a prairie climate it helps to maintain and perhaps rarely enlarges the prairie."

Assuming that fire retards forest invasion, its effect on prehistoric prairie-forest relationships would depend upon frequency and severity. Although no evidence is at hand, it is doubtful whether lightning fires were of any great importance in the prairie peninsula because rain generally accompanies lightning. Thus prairie fires would originate chiefly with the Indians. There is considerable evidence that Indians burned the prairies yearly as a means of hunting the bison, but considering the area of the prairie, and the relatively small numbers of Indians and Indian villages, it does not seem reasonable, if fire were the principal factor, that in this extensive upland prairie with its interlacing wooded streams there should be no more extensive areas of forest invasion. A reasonable conclusion seems to be that fire probably played a local role in retarding forest advance, but that its influence was secondary to other factors and has been over-stressed.

Soil Reaction. On the immature soils of the Wisconsin drift and of the deeper loess deposits the high calcium content of the subsoil tends to retard tree growth. In certain local prairies of the southeastern and southern United States also the percentage of alkaline or saline salts is high. Various authors have suggested that restricted growth on these sites is due to unavailable iron and other minor elements, to insolubility and unavailability of phosphorus, to unfavorable calcium-potassium-sodium balance, or to toxic concentrations of calcium, sodium, potassium, chloride, sulphate and other ions. Most conifers with the exception of *Juniperus* and a few others are seriously affected, especially in the seedling stage, by high concentrations of soluble salts. Among the hardwoods there are more species adapted for growth on alkaline soil (8), but these are usually not adapted to withstand heavy competition in the seedling stage. The problem is further complicated by the effect of organic matter in decreasing injury on alkaline soils and by the fact that many soils derived from limestone, chalk and marl are heavy and possess

poor internal drainage and aeration. The degree of plant injury and soil pH are also sometimes related to and vary with the moisture content of the soil (13).

In pot experiments at Ames *Pinus banksiana* died during the first season on an alkaline Webster surface soil, but grew well on acid prairie soils when inoculated with mycorrhizal fungi. Seedlings of *Quercus borealis* were

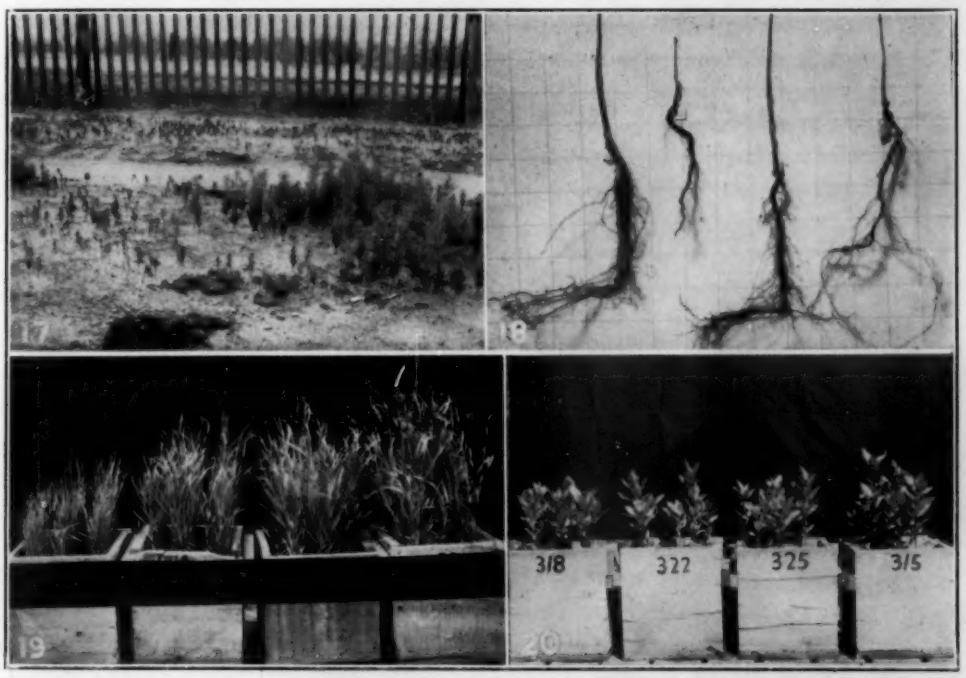


FIG. 17. Seedlings of *Picea Abies* on prairie soil. Dead and dying plants non-mycorrhizal; vigorous plants inoculated with mycorrhizal fungi from mulching material. FIG. 18. Growth of *Quercus borealis* seedlings in prairie and forest, surface and subsoils. Left to right; grown in prairie surface soil (Clarion A); prairie subsoil (alkaline, Clarion C–horizon); forest surface (Lindley A) and forest subsoil (acid Lindley C–horizon). FIG. 19. Response of *Avena sativa* on O'Neill soil to nitrogen fertilization. Left to right: none, 40, 80, and 160 lbs. NH_3 per acre. FIG. 20. Response of seedlings of *Fraxinus lanceolata* to nitrogen fertilization. Soil acid; fertilizers as in figure 19.

chlorotic, stunted, and failed to respond to fertilization on the alkaline C-horizon of a Clarion prairie soil, but were normal in appearance and responded to added fertility on the acid subsoil of Lindley (forest) or the neutral subsoil of Tama (prairie). The root systems of the seedlings on Clarion C were very poor, short and unbranched (fig. 18). Alkalinity is stressed as a factor favoring the black-land prairies of Alabama (24) and the steppes of Hungary (35). Like poor internal drainage and aeration, an

alkaline subsoil is most injurious to the deep rooted species of the forest climax.

Soil Fertility. It is considered typical of xeroseres that the climax formation occupies the most fertile as well as the most mesic sites. In the mature, till soils of the Illinoian and older glaciations the virgin forest climax soils are frequently more fertile than the grassland soils, although their agricultural value may be reduced by their greater slope and tendency to erode. In the immature soils of recent drift or deep loess deposits, however, the grassland soils tend to be markedly better, particularly in nitrogen content.

TABLE 1. *Average total nitrogen content of the surface 2,000,000 pounds of some prairie and forest soils of Iowa.*

Vegetation	Series	Texture	Nitrogen, lbs. per acre
Prairie	Marshall	Silt loam	4,029
		Silt loam	5,600
Prairie	Clarion	Loam	4,368
		Silt loam	4,986
Prairie	Webster	Clay loam	6,762
		Silt loam	8,633
Prairie	Carrington	Loam	3,756
		Silt loam	4,606
Prairie	Clyde	Silt loam	7,157
		Silty clay loam	7,929
Prairie	Grundy	Silt loam	4,253
		Silty clay loam	4,971
Prairie	Knox	Silt loam	2,117
Forest	Clinton	V.f. sandy loam	2,050
		Silt loam	2,506
Forest	Fayette	Silt loam	2,300
Forest	Marion	Silt loam	2,229
Forest	Lindley	V.f. sandy loam	1,733
		Silt loam	2,226
Forest	Ames (Conover)	Silt loam	2,150

Nitrogen analyses of important prairie and forest soils of Iowa by Walker and Brown (42) are given in table 1, and show an average nitrogen content for the prairie soils that is two or more times that of the forest soils. Note particularly the Ames soil, developed from the same parent material as the Clarion, or the Marion from the same material as the Grundy but containing in each instance about half as much nitrogen. Note also that the Knox silt loam, one of the types being invaded in western Iowa, shows a nitrogen content comparable to that of the forest soils. The high nitrogen content of the grassland soils is assumed to have accumulated under grassland cover and to be associated with the more stable organic matter forms of the prairie soils.

Nitrogen is recognized as a major fertility factor for grass development; in contrast, experiments by one of the authors have shown that tree seedlings did not respond to added nitrogen on several Iowa soils when the initial nitrogen content of the soil was more than about 2,000 pounds an acre in the surface 2,000,000 pounds of soil. The responses of two tree species to nitrogen fertilization on an O'Neill soil containing 1,900 pounds of nitrogen are compared in table 2 and in figures 19 and 20 with the responses of *Avena sativa*, used to represent a quick-growing grass. While the growth of *Avena* was increased 700 per cent on this rather infertile soil, the growth of *Fraxinus lanceolata* was unaffected and the response of *Quercus borealis* was of doubtful statistical significance.

Cowles (6) has suggested that prairie tends to change the soil in a direction which favors grass at the expense of forest. For the fertile, immature

TABLE 2. *Relative responses of a cereal grass and of two tree species to nitrogen fertilization of an O'Neill soil.*

	Dry weights of seedlings as a percentage of the check		
	Avena	*Quercus*	*Fraxinus*
None	100	100	100
40# NH_3 per acre	467	119	101
80# NH_3 per acre	801	115	95
160# NH_3 per acre	820	130	.....

prairie soils of Iowa and northern Illinois we advance the thesis that high nitrogen levels, built up in these soils during prehistoric, grassland climate cycles, are under present conditions an important factor favoring prairie species in their resistance to forest invasion. The high nitrogen content of these soils increases the density of the grass cover and results in such rapid resodding of disturbed areas that there is little opportunity for forest seedlings to become established. The dense growth and fibrous root systems of the grasses quickly remove surface moisture below the wilting point during even short dry periods. In addition they may reduce the level of available phosphorus (22) and/or other elements (45) to levels critical for tree seedling growth, and raise the carbon-dioxide content of the soil (16) to a point injurious to tree roots.

Erosion has long been recognized as having a favorable effect on forest invasion; an effect which is usually assigned to better drainage and to protection in the gullies and rough lands from the drying effects of wind. Under our theory the removal of the grass cover, and the removal of the high-nitrogen A-horizon which favors its return, become major parts of the effect of erosion. Even when the nitrogen content of eroded areas is reduced below the optimum for trees, the reduction or elimination of grass competi-

tion makes such spots available for invasion (fig. 22). The movement of invading forests along steep-banked prairie streams has probably depended as much upon this effect of erosion (figs. 11, 12, 21) as upon any single factor.

Soil Aeration. Subclimax prairie is found typically on flat alluvial or till plains, and many authors have called attention to the poor surface and internal drainage of the soils formed on these sites. Englemann (7), for example, has stressed drainage as the cause of subclimax prairie. His discussion of the prairies of Jackson and Perry counties in southern Illinois is

FIG. 21. Forest distribution along the Des Moines River, Boone County, Iowa. The Ames soil in the foreground has been cleared of forest, as have the pastures above the farther bluffs. Present woodlands are on the steeper Lindley soil. Trees on the Wisconsin till plain of the background are farmlot plantings.

noteworthy for careful observations in a district where prairie has apparently persisted for many thousands of years in a distinctly forest climate, and for its early date (1863) which enabled the writer to consult original settlers and to observe relatively undisturbed plant communities. He reports that prairie was restricted to the undissected till plains, and that these were being invaded from the rolling lands along the streams, with invasion of the narrower strips of prairie being complete. The timber on these flat lands, however, was a poorly developed growth of *Quercus stellata*, *Q. marilandica*, and *Q. palustris*, the first two considered indicative of dry and the last of

wet lands. Englemann attributed the persistence of the prairie to poor surface and internal drainage, and reported that the "post oak flats" alternated between standing water in early summer and severe drought in late summer, so that only the more resistant trees were able to exist on these former prairies. In the soils maps of Jackson county (27) the mature prairie soil on Illinoian till, thinly covered with Peorian loess, is classed as Cisne. Where the till plain has been invaded by oak-hickory timber it is mapped as Wynoose. Timber on rolling land along the streams developed the Bluford soils, and grass the Hoyleton series. Englemann reports that the Hoyleton soils, which he called "barrens," had been invaded by oak in 1860, at a rate which seemed to class their grassland cover as a disclimax maintained by fire. The level Cisne soils, however, have probably resisted forest invasion throughout most of the 150,000 or 200,000 years since the retreat of the Illinoian glacier. The force of this resistance can be judged by the fact that the bands of Wynoose soils bordering the prairie are rarely more than one-half mile wide, indicating an average invasion rate of about one foot per century.

While the Cisne and Wynoose soils are developed over level, Illinoian till, they are actually formed from a sheet of Peorian loess 3–4 feet thick (34). Ten miles south of the Jackson county prairies and post-oak flats, this same loess on unglaciated hills was covered with a luxuriant forest of *Quercus alba, Nyssa sylvatica, Liriodendron tulipifera*, and associated species, with *Acer saccharum, Fagus grandifolia*, and *Magnolia acuminata* prominent in protected sites. Transeau (37) classes *Liriodendron tulipifera* as a critical species of the eastern hardwood climax forest, yet one of the writers recalls a specimen of this tree growing on an exposed ridge of Ava loess at the south boundary of Jackson county that was 6 feet d.b.h., 90 feet to the first limb and more than 120 feet high. With climate and parent soil material identical, only topography and its effects remain to explain the sharp break between the prairies and scrub oak of the till plains and the adjoining original forest cover represented by this specimen.

Partly because of the methods of their deposition, and partly because of the type of weathering which occurs in them and the absence of erosion, flat lands tend to be fine-textured and to develop at maturity into planosols with a heavy, impervious B-horizon. If the climate is such that grass is the initial vegetation of these plains, or if the forest is destroyed during dry cycles, invasion by forest becomes difficult. In the absence of stream dissection and enough sheet erosion to carry away the clay particles formed by weathering, the difficulties of invasion increase sharply with time as the clay materials are leached downward to form a shallower and more impervious B-horizon. Prairies on flat lands thus tend to perpetuate themselves by forming planosols as well as by direct competition.

The importance of topography in soil formation is illustrated in the forest profiles formed on the loess soils of southeastern Iowa. On flat uplands, Marion soils are formed and the forest is composed of *Quercus stellata*, *Q. marilandica*, *Q. bicolor*, and *Q. imbricaria*. With slopes up to 5 per cent Weller soils are formed with a covering of *Quercus alba* and *Carya ovata*. On steeper slopes the Clinton soils support the last two plus *Quercus borealis* and *Tilia americana* as dominant species. All of these soils have developed from the same parent loess, but the level Marion has a planosol profile and a distinctly inferior forest cover which has a record of very slow invasion into the almost equally impervious prairie soils of the Edina and Putnam series. Where slope changes are abrupt the changes in vegetation are equally abrupt and the species of the more rolling lands may disappear within 50 feet.

The relationships of southern Illinois and southeastern Iowa are general, not only throughout the prairie peninsula, but for the subclimax and border line grasslands of the world. In Hungary (35), Australia (28) and Africa (11) as well as Alabama (24) and Arkansas (41), prairies on the more mature soils have been driven back to flat areas of impervious silts and clays. The prairies of Arkansas and of Louisiana for example are found on flat, heavy, Port Hudson terrace soils (fig. 25). These terraces were formed from glacial clays deposited in middle pleistocene times (40), and are therefore comparable in topography, texture, and age to the prairies of the older till plains.

Although trees of various species will grow under moisture conditions ranging from permanent swamp to semi-desert, the root systems of trees seem to be generally inefficient in both soil-contact area (fig. 18) and level of physiological activity. It seems probable, therefore, that it is not poor drainage alone, or even alternating wetness and dryness, which limits forest growth on these prairie soils, but rather the unfavorable oxidation-reduction relationships of fine-textured, wet soils. Thus we find the well aerated Knox and Monona soils of western Iowa invaded much more rapidly than the impervious Cisne of southern Illinois; in central Iowa the deep, frequently rather sandy soils of the Clarion series on Wisconsin till have been invaded more rapidly than the impervious Putnam soils formed on the older Peorian loess over Kansan till in southern Iowa, and throughout the prairie-forest borderline small differences in elevation, drainage, and aeration markedly affect forest invasion (figs. 24, 25).

Patton (28) stresses soil texture and topography as major factors in the distribution of grasslands and forest in Victoria. Forest is reported on the coarser-textured soils, even when rainfall conditions are unfavorable, while subclimax prairie persists on impervious plains. Stoeckeler and Bates (36) ascribe the beneficial effects of sandy soils in the shelterbelt region to their

greater free moisture content. Turner (39) stresses soil aeration as an important factor affecting growth rates of trees. Under critical conditions poor growth means poor survival, and we feel that poor soil aeration, due to poor surface drainage and particularly to impervious, clayey soils, is the most important single factor restricting the spread of forests and favoring the persistence of subclimax prairie throughout the world.

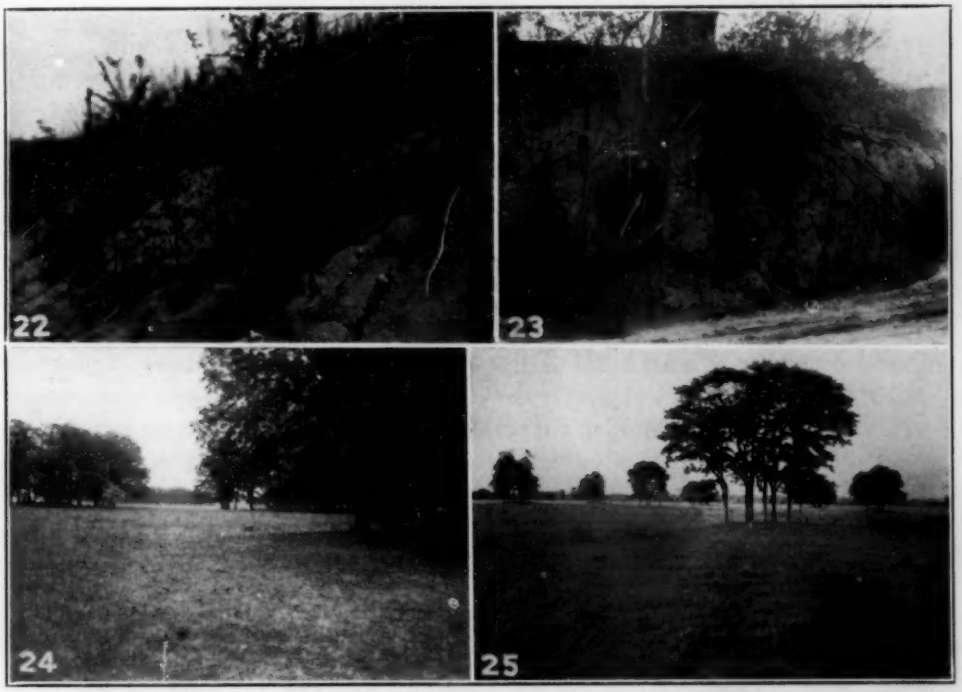


FIG. 22. Pure stand of *Ulmus americana* on subsoil exposed in road cut; west exposure; no evidence of seepage. Jasper County, Iowa. FIG. 23. Exposed roots of *Quercus macrocarpa* in western Iowa. Medium-sized roots were abundant at the 9-foot level. FIG. 24. Oak-hickory forest on swells of the more porous Clarion soils with swales of compact Webster originally in low prairie. Boone County, Iowa. FIG. 25. Trees on hummocks; Port Hudson Terrace prairies of southeast Arkansas.

The effects of soil aeration on forest-prairie competition cannot be explained until we know more about the physiology of roots and particularly of tree roots. A space factor is undoubtedly concerned, with the heavier growth of the forest requiring a deep root system for an adequate water supply during periods of stress. It seems probable, however, that questions of fine root growth and level of physiological activity are involved; that tree roots are relatively inefficient and, in some of the more xeric species at least, susceptible to the effects of oxygen deficiencies (15) or carbon dioxide

accumulations (18). If it should develop that the roots of the more xeric hardwood forest trees are particularly susceptible to carbon dioxide accumulation, the data of Howard (16) would gain added significance to the problem of invasion of the prairie. He found soils under grass containing up to five times as much carbon dioxide as his cultivated control soils. Such an accumulation in soils of compact structure and slow rates of gas exchange might be the determining factor in the survival of tree seedlings in sod.

DISCUSSION

Pollen analyses from all parts of the prairie peninsula are in agreement in showing a very general spread of northern coniferous forests throughout the region during each of the glacial periods. In Iowa pollen analyses (20) and buried soil profiles (33) show that the interglacial periods have been dominated by grass rather than by deciduous forest, indicating that the soils and/or climate of the state have not been generally favorable for invasion by southern forest species during pleistocene times.

Picea forests were present in Iowa following the late Wisconsin glaciation and may have been general. Unfortunately for our studies, most peat deposits are surrounded by moraines or other formations relatively favorable to forest. *Picea* will grow, however, in flat, wet soils, and pending analyses of peat from the open till plains the authors are inclined toward the assumption that these also were at least partially covered with coniferous forests. Such an assumption must account for the absence of any residue of a forest profile in the prairie soils. The prairie fauna, from earthworms to badgers, is so predominantly burrowing, however, as to seem able to rework shallow profiles in the period available.

With rising temperatures the spruce forests should have been replaced by oak-pine or oak. Instead *Pinus* pollen never exceeded five per cent at this stage in Lane's Hancock County bog (19), and *Quercus* pollen was exceeded by grass and weed pollens indicative of a savanna rather than a closed forest. It seems highly probable that the till plain went directly to prairie during this time, as it apparently had during earlier interglacial periods. The high initial lime content of the till plain, and its flat topography without protected or disturbed areas for ready invasion, as well as its poor soil aeration, would have favored grass rather than oak during this increasingly xeric period.

In the 8th and 7th feet of Lane's bog, graminaceous pollen increased from 23 to 60 per cent and *Quercus* dropped from 20 to 4 per cent. Such a change clearly indicates a severe dry period. It is noteworthy that *Quercus* pollen averaged 4 per cent from the 7th foot of this bog to the top, suggesting that pollen was coming from the groves still present in the lee of Twin Lakes one to two miles north and west of the bog. Many data indicate that this dry

cycle was general; its probable date, 5000 to 8000 years ago. During this dry period grass undoubtedly became established on much former forest or savanna occurring on morainal hills and eroded slopes. The Hoyleton soils of southern Illinois and the morainal hills of northern Illinois may well have been deforested at this time, and the forests driven back behind the streams, lakes, and other fire-breaks, or to protected areas, that are mentioned above as showing in the distribution of mature forest soils but not always in the more recently established, original forest cover.

Although pollen analyses indicate a more mesic period between about 4000 and 1600 years ago, soils data from central Iowa indicate that the climate was in the main that of a grassland climax with only limited forest invasion during the period. A generally warm-dry climate during the Middle Ages is reasonably well documented by tree rings, historical records, Nile valley floods, remains of the Greenland settlements, etc. (4). The end of this dry cycle at about 1100 A.D. probably marked the beginning of the current forest climax climate for Iowa and the western base of the prairie peninsula.

During the last 700 or 800 years forests had covered townships in northeastern Iowa, advanced one to four miles from the main streams of central Iowa, and advanced as scattered trees and clumps in western Iowa at the time of settlement of the state. The disturbances of settlement, mainly, we feel, periodic over-grazing of prairies and pastures, have resulted in spectacular forest advances in western Iowa during the last 50 years. The early advances were as rapid as could have been expected against the competition of established and vigorous prairie sod, but they were limited to deep, well aerated soils. Swales of poorly aerated Webster soils were by-passed in central Iowa (fig. 24), and invasion of mature or nearly mature planosols in southern Iowa and Illinois was negligible. Afforestation, including recent invasion, in western Iowa has followed a belt not far behind the Missouri river bluffs which perhaps represents a gradation of the loess (34) into particles neither too coarse and therefore dry, nor too fine and poorly aerated.

The remainder of the prairie peninsula remains, as it probably has during most interglacial time since the Aftonian, a subclimax or edaphic climax maintained primarily by its flat topography and its impervious, poorly drained and poorly aerated soils. If the present climate lasts for the necessary millions of years until the till plains are dissected and their heavy surface and subsurface soils eroded away, we may expect the disappearance of the prairie peninsula.

SUMMARY

Undisturbed Iowa forests survived the recent drought years without injury, and forest is spreading and maintaining itself throughout the state

under present climatic conditions. Oak-hickory forest is therefore considered to be climax, from a line somewhere near the Missouri and Little Sioux rivers eastward. In western Iowa, where the climate approaches that of a prairie climax, soil factors become increasingly important, and forest potentialities are limited to the coarser-textured, better aerated soils. Forest in this area requires no protection, however, from the full force of sun and wind under present climatic conditions, and is currently invading both disturbed and undisturbed areas.

General and local evidence from glacial varves, tree rings, pollen analyses, soils distribution, and other sources indicates that the climate of Iowa during late-glacial and post-glacial times has changed from boreal through oak-hickory forest climate to grassland climate, and that the current forest climate has probably existed for only 700 to 800 years. For perhaps 5000 years preceding this recent shift the climate of Iowa was predominately that of a grassland climax, with the forest driven back to areas of deeper soils sheltered from fires and prevailing winds.

The prevalence of prairie in Iowa and Illinois is not, however, due to this recent xerothermic period, but dates probably to the soils disturbances initiated by the first or Nebraskan glaciation. The prairie peninsula is considered to be a subclimax associes maintained by the soils and topography of the glacial till plains. On the unleached soils formed from deep sheets of Peorian loess and Wisconsin till, the high lime content of the soils and past xerothermic periods have favored prairie grasses and legumes which have in time built up a high nitrogen and organic content in these soils. This content now stimulates the growth of grasses at the expense of invading tree seedlings. On the leached but undissected till plains of the Kansan and Illinoian glaciations, planosols of poor surface and internal drainage and aeration have been developed which are distinctly unfavorable for trees, particularly under border-line climatic stresses. Planosol prairies are invaded very slowly and only by the more xeric forest species, even with a distinctly forest climate, and their transformation to oak-hickory climax will probably require extensive erosion to establish drainage and permit development of new and less mature soil profiles. These prairies may therefore be considered to be a semi-permanent, edaphic, but not climatic, climax.

The invasion of forest along streams, which has been cited as evidence of a forest postclimax dependent upon protection, is considered to be related in the older soils to increased drainage and soil aeration, and in the less mature to the removal of the high-nitrogen surface soils which are relatively much more favorable for the growth of grass than of the slow-growing and vulnerable tree seedlings.

The relationships shown for Iowa are present throughout North America and in Europe, Africa and Australia. In local areas prairies are maintained

by sandy or gravelly soils too dry to support forest. The vast bulk of the peninsula and of other subclimax prairie, however, is found on silty or clayey plains of glacial, alluvial, or other origin. Poor soil aeration caused by fine-textured soil and poor drainage is probably the most important factor in the persistence of these subclimax prairies.

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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 71, No. 1, pp. 77–92 JANUARY, 1944

MORPHOLOGICAL OBSERVATIONS ON THE TOMATO PLANT[1]

F. W. WENT

Even though a number of papers have been published on the abnormal morphology and teratology of the tomato plant (Caldwell 1930, Dana 1939, Masters 1869, Penzig 1894, Rischkov 1938, Schlösser 1936, Worsdell 1915) there are surprisingly few in view of the importance of the tomato as a major crop plant on the one hand and its uncommon variability in a morphological sense on the other hand. During the last four years about two thousand full grown tomato plants and 40,000 seedlings were observed in the greenhouses of the California Institute of Technology, grown in part under well controlled conditions, and in the following article morphological observations on these plants will be described. Some of these observations were systematically carried out on all plants, but those on the rarer teratological cases were entirely incidental.

Most observations were made on "San Jose Canner" tomatoes, *Lycopersicum esculentum*, but additional work on "Marglobe" and other varieties has shown that many of the described phenomena are not restricted to one variety only. The tomato seeds were sown in flats in washed sand, 100 per flat, and were watered with nutrient solution after germination. The almost complete absence of any segregation of such characters as dwarf, potato-leaf, yellow leaf, and the great uniformity of growth-rate and response to external factors (Went 1943) all point towards the essential homozygosity of the seed. The abnormalities were found in ever changing proportions, indicating that they were modifications and not genetically determined. Moreover, most of these abnormalities occurred only in one stage of development, and before and afterwards the plants were perfectly normal.

Seedlings. During germination the two cotyledons unfold and enlarge. Syncotyly is very rare (less than 1 in 1000) and tricotyly is rarer than in most plants (8 in 3300). About one week after germination the first two foliage leaves, which were already initiated in the embryo, grow out. Occasionally (less than 1 in 2000 plants) these two first leaves have merged into a beaker-like structure or even into one peltate terminal leaf, without trace of a terminal bud between them. A cotyledonary bud develops in such plants and takes over the main stem function. In such cases the two leaf primordia

[1] The author is indebted to Mrs. M. O. Carter for the preparation of the drawings in this paper.

must have merged and overgrown the terminal meristem. This was never observed in any other stage of development of tomato plants.

The following most remarkable abnormality was observed three times: After normal germination the first two foliage leaves developed. No terminal nor axillary buds were present; even under the microscope no trace of them was visible. Therefore these seedlings did not develop beyond the two-leaf stage. But both cotyledons and leaves continued to grow in surface and thickness. Instead of falling off after a month the cotyledons remained alive and attached to the plant throughout its life span, which was 3–6 months. The root system seemed perfectly healthy and normal, and well developed. Similar cases were described by de Vries (1903, p. 322) for *Helianthus*, *Pentstemon*, and *Cannabis*. Apparently these seedlings had completely lost the ability to form buds anywhere. In normal plants decapitation and debudding lead to the formation of numerous adventitious buds on the callus overgrowing the wounds and on the upper surface of the leaf rachis. But these budless seedlings showed no trace of such regeneration. Nor did they regenerate anything but a slight callus on wounds produced on leaves or stems, even after treatment with auxin paste.

Two seedlings were observed which were completely budless, like the ones just described, but lacking even the two primary leaves. They consisted only of roots, a hypocotyl, and two cotyledons.

Phyllotaxis. The leaves of the tomato are inserted on the stems with a typical 2/5 divergence (Hayward 1938; sometimes referred to as 3/5: Caldwell 1930, Schlösser 1936). There is no favored direction of the foliar spiral: out of a group of 50 plants 25 had a left- and 25 a right-hand spiral. It seems to be entirely left to chance where the larger gap between the first four leaf primordia appears. As mentioned before, the first two foliage leaves are practically opposite and develop simultaneously; the next two leaves are sometimes almost opposite, but more often they are inserted at different levels and have a divergence of less than 180°. Beyond that a normal 2/5 spiral appears.

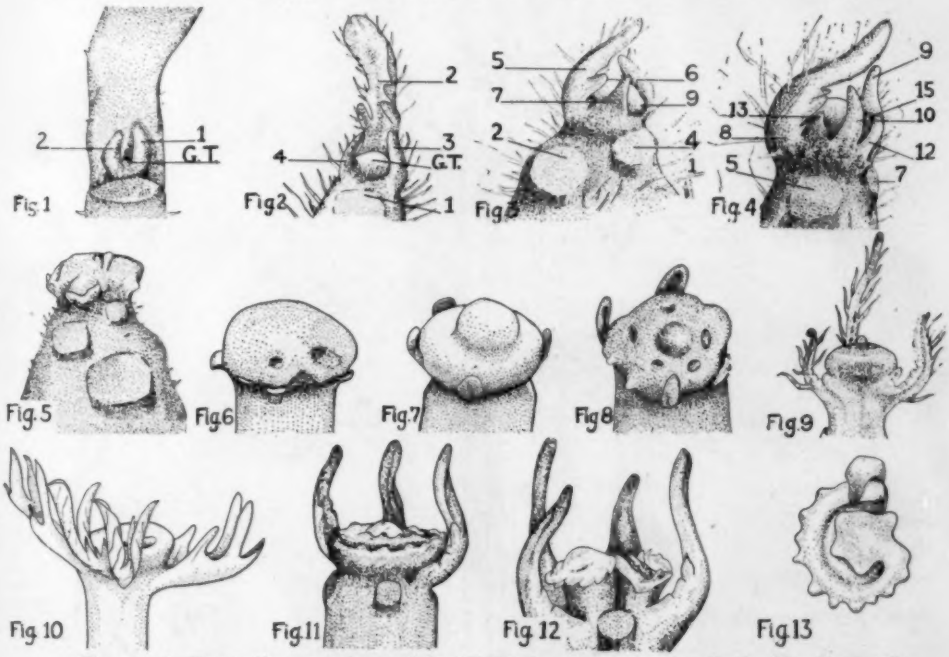
In 17 of 2200 seedlings the first two leaves were not opposite, and a regular 2/5 phyllotaxis started actually with the first leaf. Almost all these 17 plants were taller than those with opposite primary leaves.

In tricotyly the first three leaves develop simultaneously and are of the same size and are practically whorled, alternating with the three cotyledons. In one plant three whorls of three leaves each developed after the three cotyledons. Immediately above the third foliar whorl the stem was bifurcate, the two branches having normal foliar spirals in opposite directions.

In more than 90 per cent of all plants the direction of the foliar spiral does not change up to the first flower, so that the direction once established

in the seedling persists. But in less than 10 per cent a reversal of the foliar spiral occurs between the fifth and fifteenth leaf. Lateral shoots from the man stem have an equal chance to follow a left- or a right-hand spiral, irrespective of the direction of the foliar spiral in the main shoot, and no pattern in their appearance was found. This also attests that the left- or right-hand character of the foliar spiral is fortuitous, and is not an inherent or inherited characteristic of each individual.

When the seedling shoot emerges from the soil, microscopical examination shows only two opposite leaf primordia enclosing a flat and very small

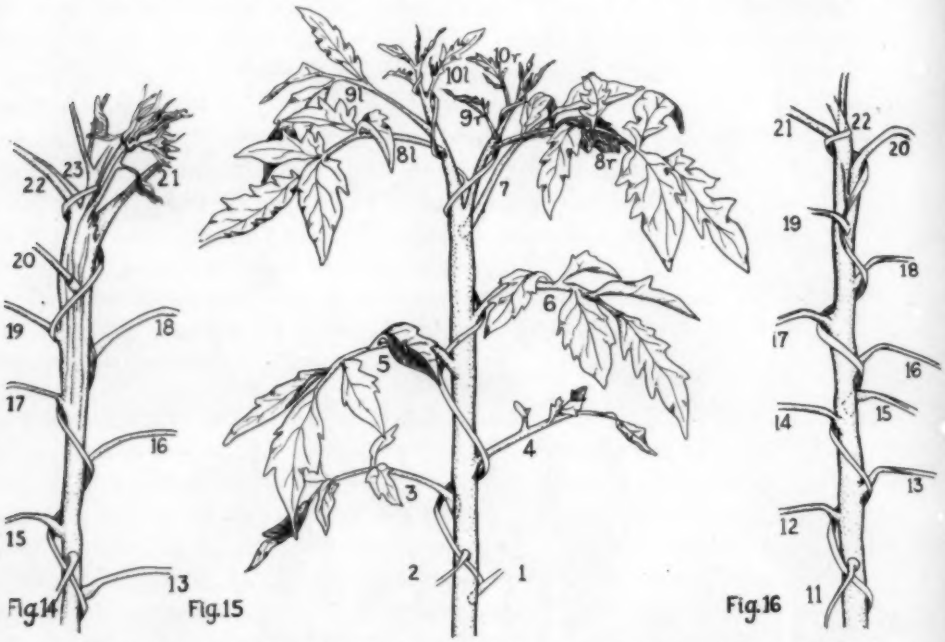


FIGS. 1–4. Vegetative growing points (G.T.) in young tomato plants. Numbers refer to order number of leaf primordia. The larger leaves have been removed and their scars are numbered. FIG. 5. Normal flower primordium (fasciated) formed after 16th leaf primordium. Lateral flower primordium without subtending bract just below terminal flower. FIG. 6. Flower primordium, arrested in further development, formed after 4th leaf. FIGS. 7 and 8. Flower primordia laid down after 7th and 8th leaf. FIGS. 9–13. Flower primordia formed after 10th–13th leaf.

growing point (G.T. in figure 1). From the next stage on, when the first leaves are just starting to expand and are only a few millimeters long, the growing point is dome-shaped, and the leaf primordia appear in spiral order some distance below the dome. Figures 2, 3, and 4 show the growing point in different stages of vegetative development of the plant. The leaves are numbered in the order in which they appeared on the growing point. These figures show that the primordia are never in contact with each other, and

throughout their development remain separate. After 14–20 leaves have been initiated, the growing point broadens and is transformed into a terminal flower primordium (fig. 5). Occasionally, as seen in this figure, a small number (1–3) of lateral flowers are initiated as axillaries of bracts and thus continue the foliar spiral. The subtending bracts of these lateral flowers may or may not be apparent, and under the proper conditions (high night temperatures) these bracts can develop into normal leaves (cf. Went 1943).

In some plants the direction of the foliar spiral reverses without any apparent reason. One such case is shown in figure 15, in which the spiral was



FIGS. 14 and 16. Exceptional foliar insertion on young tomato plants below their first inflorescence. Whereas up to the 18th or 19th leaf a normal right-hand $\frac{2}{5}$ spiral exists, indicated by the ribbon following the insertion, (leaf 18 just above leaf 13), this spiral reverses for the next 5–3 whorled leaves. Stem becomes much creased above 18th leaf. Axillary shoots from the highest leaves not drawn. FIG. 15. Dichotomy of tomato stem. Right hand foliar spiral up to fifth leaf, beyond that left hand spiral which continues in both shoots.

right-hand up to the fifth leaf, but beyond that changed to left-hand. In other cases, like in figures 14 and 16, the spiral reverses in connection with the formation of the first flower, which will be discussed later.

Figure 15 also shows another abnormality, namely, true dichotomy of the stem. Caldwell (1930) also described dichotomy in tomatoes. Although many authors (e.g., Velenovsky 1905) reject the existence of true dichotomy in angiosperms, the case of figure 15 seems well-founded. After the seventh leaf

the stem branches into two almost equal forks, each with a normal phyllotaxis. In both the same left-hand spiral of the 5th–7th leaf is continued. All leaves, including numbers 5, 6, 7, 8r, 8l, 9r, and 9l have normal axillary buds, so that neither of the shoots can be considered an axillary shoot. Besides, no trace of a flower primordium or aborted leaf is visible. This is important, since in the tomato most cases of apparent di- or trichotomy arise in connection with flowers, and are axillary buds from opposite or whorled leaves just below the flowers, while the main axis is terminated by the flower.

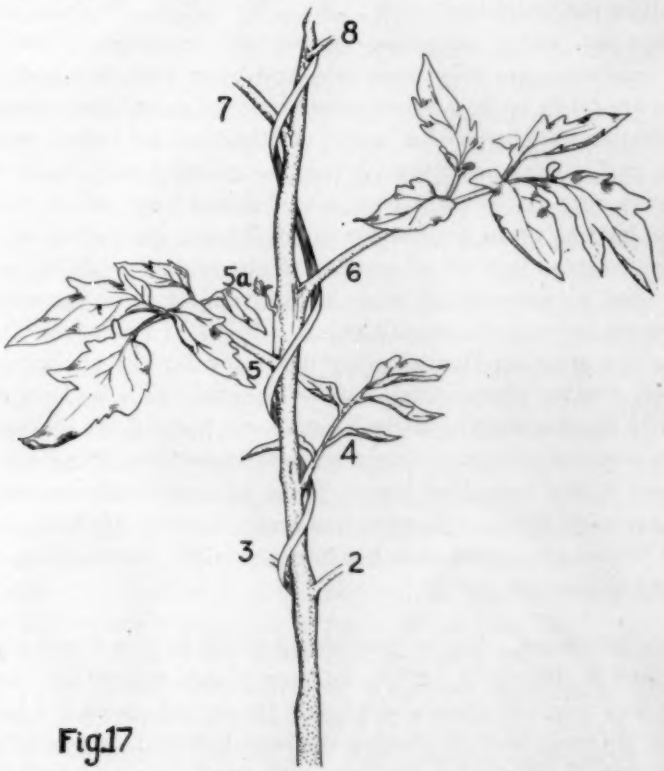


FIG. 17. Adventitious leaf (5a) not interrupting foliar spiral.

In not more than 10 per cent of the plants which develop dichotomy, an apparent duplication of the leaf immediately below the bisection was visible. In such cases the petiole was inserted with a wide base, and two axillary buds were visible. The end leaflet of this leaf was bifurcate. Here a true connation of two leaves existed. A similar case has been observed in a seedling with the two first foliage leaves grown together along the petiole, and having a forked end leaflet. In one case connation of two opposite leaflets was found. They emerged as one leaflet on the adaxial side of the leaf rachis,

but were still clearly recognizable as two since farther up the leaflet was forked.

Once a true adventitious leaf was observed on a tomato stem (fig. 17). It was very small, consisting of only three minute lobes on a thin petiole, and it did not interrupt the foliar spiral. There was a normal 144° divergence between the leaves immediately below and above the adventitious leaf. An explanation of this case seems simple on the basis of a vertical duplication of a leaf primordium, since the adventitious leaf was inserted almost exactly above the lower leaf.

Another interesting phenomenon observed in tomato plants whenever growing conditions are very favorable, and when both day and night temperatures are fairly high, is the disappearance of apical dominance. As soon as the tomatoes have reached a height of 30–40 cm. all lateral buds start to grow out, and continue to grow. A number of them may reach almost the same growth rate as the main stem, which is not markedly inhibited in its growth as long as there are not too many laterals competing with it. This phenomenon occurs only when aeration of the roots is optimal, as in gravel or coarse sand, or when enough roots have developed above the nutrient solution on plants grown in water culture.

Under the same conditions as are necessary for the abolition of apical dominance, another phenomenon can be observed. This is the formation of from few to many adventitious buds on the rachises of the leaves. This bud formation becomes pronounced only when the growth of lateral shoots is prevented, and it starts on older leaves. These adventitious buds can grow out into normal leafy shoots, but when too many develop per leaf they remain smaller. The same phenomenon has been described for tomatoes by Penzig (1894) and Gustafson (1937).

Flower Initiation. The various stages of the tomato flower primordium are described by Hayward (1938). In older plants flowers may be observed in almost any stage of development, but young plants do not form flower primordia unless at least 13 leaves have been initiated. In exceptional cases (1–5 per cent of all plants) tomatoes will produce a terminal flower primordium in an earlier stage of development. These primordia, however, never develop into normal flowers but remain arrested in their growth at some early stage of differentiation, although the rest of the plant continues to grow. The meristematic cells of such a flower primordium remain isodiametric but enlarge to some extent, so that a stationary and magnified model of a young flower is produced, which abruptly terminates the stem. The internode between primordium and highest leaf may be as long as or longer than the preceding one, so that when the flower development has not progressed so far that the sepals are growing out, it appears as though the main

stem of such a plant had been cut off with a sharp knife. Such abnormal plants are easily recognized in somewhat later stages when the axillary buds of the upper leaves start to grow out. Sometimes some or all of these terminate in the same way. But the stem developing from the highest normal bud will be entirely normal, proving that the abnormality is a modification, and not genetically determined.

In the most extreme cases, observed only a few times, the flower primordium was produced after the second to fourth leaf. One such case is shown in figure 6. The calyx primordia are barely indicated. The meristem has remained indefinitely in the semimature condition, but is clearly different from the rest of the stem tissue in that no hairs or glands have developed on it. The primordia shown in figures 7 and 8 terminated the main stem after about 7 leaves had been formed. The sepals are further developed, and indications of petal primordia are present. When the plants were slightly older before the flowers were formed, almost invariably the sepals started to differentiate as foliage leaves, as indicated by the lateral lobes at their base, which are always absent in sepals. Figures 9, 10, 11, and 12 show such sepals. The transformation to leaves has not been complete since they have not grown out further. In such primordia the place where the carpels should develop is mostly occupied by an undifferentiated meristem, sometimes superficially pitted, the number of pits corresponding with the number of sepal primordia. This phyllody of the calyx can also be observed in lesser degree in normal flowers, especially of plants grown in low night temperatures. Schlösser (1936) has investigated a genetically determined case of phyllody, and Dana (1939) stressed the correlation between virus attack and phyllody of calyx.

In primordia formed from the ninth leaf on, the meristem from which the flower differentiates enlarges to such extent that fasciated flowers or primordia result. Usually the number of sepals is still five, but all other flower parts have considerably increased in number. All different stages have been encountered, from a simple ribbon-like widening (fig. 12) to spirals (fig. 13) and complete ring structures (figs. 10, 11). In the latter petal and stamen primordia are formed both along the outside and inside of the ring-like meristem. In a few primordia (figs. 7, 11) the center of the meristem protrudes in a manner suggestive of continuation of the stem meristem, but not a single instance has been observed in which a recognizable stem was formed in the center of a flower. For this reason it is doubtful whether this central protrusion, which never shows further differentiation, has any morphological significance.

The later the first flower primordium is laid down in the development of the plant, the stronger is the fasciation. Therefore the first flower which fully develops is invariably strongly fasciated. Anywhere from 15 to 50

carpels may develop. Masters (1869) mentions syncarpy. Masters and Penzig consider many of those fasciated flowers as synanthia, but others are due to the natural variability in number of flower parts in the tomato. These supernumerary carpels are arranged, as would be expected from the primordia just described, either in single or branched ribbons, or in rings. In the latter case the center of the flower is occupied by a whorl of sepals, followed centrifugally by whorls of petals, stamens, carpels, stamens, petals, and sepals. Such a case was also described by Rischkov (1938).

Fruits from fasciated flowers are invariably larger and heavier than ordinary fruits which weigh 100–200 g. The heaviest fasciated fruit which developed weighed 675 g. Its shape was comparable to that of a brain, since the ribbon of carpels was folded and branched like the convolutions of this organ. When lateral flowers and fruits are present in the first flower cluster, the fasciation of the end flower is never so extreme as when the latter is solitary. The lateral flowers are mostly normal 6-merous.

It seems that differentiation of carpels is only possible when at least 12 foliage leaves have been formed since germination. With the presence of carpels the full development of sepals, petals, and stamens is correlated. As an exception to the latter rule the first sepals may change over, after their initiation, to foliage leaves. The greater the number of foliage leaves already present on the seedling, the larger these transformed sepals grow before their development is stopped. Examples are seen in figures 10, 11, and 12. In the more advanced stages even an axillary bud is present above each sepal (fig. 9) and the stem axis between the sepals and the primordium starts to elongate. This was also observed by Masters (1869, "apostasis"). Frequently, after the initiation of this whorl of 3–5 calyx lobes transforming into leaves, the growing point forms a new complete and strongly fasciated flower, which usually does not carry lateral flowers. Therefore in a varying percentage of plants, and most frequently in plants growing in high night temperatures, the first flower is surrounded by 3–5 more or less whorled leaves. Such cases are shown in figures 14 and 16. The insertion of these upper leaves at approximately the same height indicates that they do not belong to the ordinary foliar spiral. The following other arguments in favor of their initiation as sepals can be adduced:

1) The stem below these whorled leaves is not round, but strongly creased and lobed on cross-section (fig. 14).

2) In one group of 40 plants 34 had 16–20 leaves in a normal foliar spiral below the first flower. Six plants had an irregular more or less whorled leaf arrangement below the first flower. All of these had 22–26 leaves, of which 17–19 were placed in a normal foliar spiral, and the upper 3–7 were whorled. Figure 18 shows the distribution curve of the number of leaves below the first flower, and gives clear evidence that the whorled leaves are "extras."

3) Still clearer proof of the different nature of the 3–7 whorled leaves in the six exceptional plants is found in their arrangement. They are not placed in a perfect whorl, but some are inserted higher than the others. In this way a spiral may still be traced through them. In only two of six cases the spiral through these extra leaves was continuous with the foliar spiral in the lower part of the stem, but in the other four cases the spiral changed from left to right or the reverse after the 18th or 19th leaf. Such a reversal in spiral between foliage leaves and sepals is not uncommon and it proves that these upper 3–7 leaves are not started as leaves in the ordinary cycle of leaf initiation in the growing point but belong to a different morphological series.

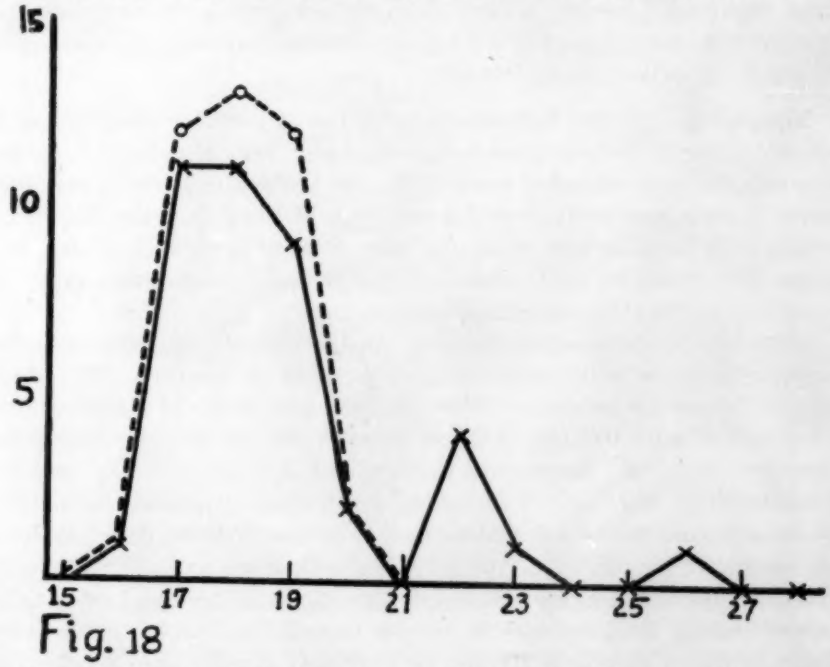


FIG. 18. Frequency (ordinate) of tomato plants having different numbers of leaves (abscissa) formed before the first inflorescence (crosses and solid line). When the whorled leaves are not counted the broken line and circles give the frequency distribution.

The described abnormalities in phyllotaxis have not been observed below the higher flower clusters in the San Jose Canner tomato.

An experiment was carried out in an ordinary greenhouse to determine whether the presence of a particular leaf or number of leaves was required for flower initiation. In an early stage, when only two fully developed leaves were present on the plants (meaning that the 10th leaf primordium had just been laid down), all leaves were pulled off as soon as they had reached full size, and only a few leaves were left. Whereas this had a pronounced effect

on stem elongation, it hardly affected organ initiation in the growing point and the flower primordium was formed after the 15th–16th node irrespective of the number of leaves and the type of leaves left. This is another indication that flower initiation in the tomato is a "morphological" process, independent of external conditions, and occurs after the growing point has gone through the cycle of leaf initiation for 15–16 times.

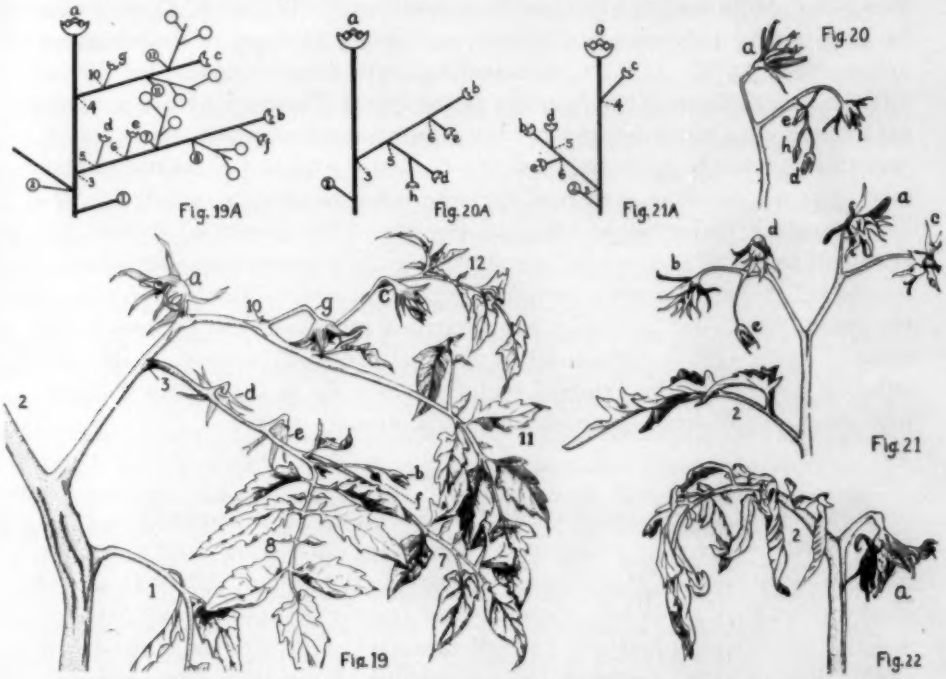
Only one plant was found which did not conform to the above mentioned rules of flower formation and differentiation. Its solitary flower primordium was initiated after the 7th leaf, but nevertheless developed into a normal flower. There were no functional axillary buds in the leaf axils, so that the plant remained 7-leaved. Normal fruit set occurred after anthesis. Only after the fruit started to grow did adventitious buds appear on a small callus formed in the axil of the highest leaf.

Morphology of the Inflorescence. Upon superficial observation the morphology of the tomato inflorescence may seem very complex. It may be a cyme or a simple or branched raceme, leafy or leafless, terminal or seemingly lateral, purely generative or with many vegetative axillary shoots. Various investigators have already explained part of these variations (Crane 1916, Yeager 1927, Bouquet 1931) and including the present observations all can be reduced to the following simple scheme.

After the development of a limited number of leaf primordia the apical meristem broadens and transforms into a flower primordium. This is contrary to Cooper's observation (1927) that the first flower of a cluster forms in the axil of a leaf. If this is the first flower formed on the young plant, sometimes no lateral flowers are present, and a single strongly fasciated flower develops. More often a few of the lower organ primordia on the main axis have become flower primordia (fig. 5). In that case the flower insertion continues the foliar spiral of the shoot, since they are axillary buds in the axils of leaves, which either are still discernible as subtending bracts or are entirely lacking. To complicate the picture these laterals may either be single flowers so that a raceme is formed, or they may develop into 2–3-flowered shoots giving rise to a cyme (figs. 20, 21).

In normal cases the lateral bud of the leaf immediately below the lowest flower primordium is purely vegetative, and after growing out, takes over the main axis of the plant, forming a sympodium. Generally this lateral bud grows up united with the lower portion of the leaf stalk (when pulling a young leaf off the shoot, the lateral bud usually remains attached to the leaf) so that the inflorescence seems to emerge laterally from the shoot, without a trace of a bract (fig. 19). But invariably the leaf opposite the inflorescence does not have an axillary bud, proving that the shoot above this leaf is lateral. There are varietal differences in the number of leaves formed on these lateral shoots before the apex becomes generative again, so that in the

San Jose Canner tomato an inflorescence appears regularly after every fourth or fifth leaf, whereas in other varieties 2 or 3 leaves are formed between inflorescences. This number is independent of the variations in external conditions (nutrition, day and night temperatures, light intensity or duration) as used in present experiments. This was more or less to be ex-



FIGS. 19–22. Tomato flower stands as developed under different night temperatures; day temperature, 26.5° C. All apical flowers (a) are fasciated. Figures 19A–21A are hypothetical reconstructions of the branching of these flower stands. A circle stands for a leaf, a dotted line for a bract, and a half circle for a flower. FIGS. 19 and 19A. Night temperature 26.5° C. Highly vegetative inflorescence. Main shoot terminates in flower *a*. Leaf 2 and its axillary shoot (which has become main axis) connate. Bracts 3 and 10 and still visible, bracts 4, 5, and 6 are completely absent, and bracts 7, 8, 11, and 12 have grown out into normal leaves. Axillary buds of bracts were transformed into flowers, of leaves remained vegetative. It is possible that flower *e* instead of flower *b* terminates the axillary shoot of bract 3, and that the shoot bearing flowers *b* and *f* and leaves 7 and 8 is a secondary shoot in the axil of (hypothetical) bract 6. FIGS. 20, 20A, 21, and 21A. Purely generative inflorescences developed in night temperature of 12° C. No trace of subtending bracts can be found. FIG. 22. Night temperature 7° C. Only terminal flower has developed on inflorescence.

pected, since otherwise such characters presumably would not have been recognized by Schlösser (1938) as based on genes.

When the inflorescences develop while the plants are subjected to high night temperatures (20 or 26° C) the lateral shoots below the apical flower pri-

mordium are partly leafy, and terminate in 1–3 flower primordia each (fig. 19). This gives rise to a remarkably complex inflorescence, for in each leaf axil a lateral bud develops bearing some leaves and a terminal flower. This leads to a profusely branched leafy inflorescence, with mostly solitary flowers scattered all through it and seemingly arising laterally from its axis. When the plants are kept at night temperatures of 10° and 5° C, no leaves develop on the inflorescences, which are simple racemes or few-flowered cymes (figs. 20, 21, 22). At intermediate night temperatures (15° C) an intermediate number of leaves grows on the cymes. These temperature effects are evident only many weeks after the plants have been exposed to them, so that transfer of the tomatoes from one to another night temperature treatment does not result in change of the inflorescences already initiated.

Temperature also has an effect on the size of the developed flowers, but low night temperatures or low light intensities do not materially decrease the number of flower primordia initiated per inflorescence. This means that in the tomato the flower initiation is primarily a morphological process in the sense of Sachs (1893), influenced by internal organization and genetic constitution rather than by external factors. Flowering in the tomato is photoperiodically indifferent, as confirmed in the present work.

DISCUSSION

Many of the phenomena described in this paper are abnormalities, or in other words, occur only occasionally. This does not reduce their value for morphological considerations: on the contrary, the author feels that all the observations have given him a much better insight into the normal development of the tomato plant and the potentialities of its meristems. Rischkov (1938) has recently discussed the importance of teratology for morphology and developmental mechanics in plants and concludes: "Teratological phenomena make possible the investigation not only of the prospective potentialities of different plant organs, but also of the phenomena of correlative and autonomous differentiation, of polarization of the meristem, etc."

All described observations of the morphology of the tomato plant not only give a better understanding of its development, but also contribute to morphological concepts. They strongly support the views of Sachs (1893) that we have to distinguish between initiation, determination, elongation, and maturation in the development of an organ. It has been shown that leaves can be initiated either as leaves in a normal 2/5 spiral, or as calyx lobes approximately in a whorl. The second developmental stage, determination, decides the nature of the initiated organ. It was found that neither initiation nor determination is affected by the external conditions which are most important for fruit-set and vegetative development of the tomato. This is exactly what Sachs meant by grouping initiation and determination to-

gether as the morphological stage, when development is ruled by internal forces such as genetic constitution, and is rather independent of changes in the external conditions. The elongation and maturation on the other hand (Sachs' physiological stage) is almost entirely dependent on the prevailing conditions of the surroundings, especially night temperature (Went 1943). In addition we have to distinguish between the vegetative growing point and the flower meristem into which it is transformed after the first 13–17 leaves have been initiated. No external conditions were found to influence this transformation. In fully developed plants the transformation of the apical meristem and of the higher laterals occurs regularly after initiation of 4 or 5 leaves, but in young plants 13 or more foliage leaves must have been initiated before a flower can fully develop. In exceptional cases the transformation may take place earlier in the life of the tomato plant, but then initiation and determination of the flower-parts is defective and does not proceed beyond an early stage of development. Independently of the poor organ development the generative meristem widens and enlarges proportionally to the number of previously initiated leaves. It almost seems as if the plant continuously forms a limited amount of material required for the formation of a flower meristem. This usually is released for the first time after the 13th–17th leaf, and is then in such excess that a fasciated flower results. Completely independent of the materials for flower meristem formation are the determination factors for the different flower-parts. They become available in sufficient amounts only after the 13th–17th leaf. Earlier the calyx primordia only develop, with the aid of leaf growth factors, into seemingly normal leaves, but although a large flower meristem is present and organ primordia are initiated, they do not develop into petals and stamens.

The observations also strongly support the view of Grégoire (1938) on the nature of the flower. No facts were found which support the idea that the tomato flower is a foreshortened vegetative shoot. On the contrary, phyllotaxis is not continuous from normal foliage leaves to leaves transformed from calyx lobes. The meristem of the flower is radically different from the vegetative growing point: whereas the latter very seldom broadens into a fasciation, and rarely widens enough to cause the stem to branch dichotomously, the first flower primordium is invariably fasciated. But notwithstanding the great plasticity of the flower meristem no reversion to a vegetative meristem was ever observed in these tomatoes.

In view of these facts it seems desirable to extend Sachs' scheme of growth of the stem and its derivative organs as follows:

A. Meristematic or morphological stages. Growth mainly by cell division; largely independent of external conditions. (Some exceptions to this rule are noted.)

1. *Transformation.* Meristem as a whole is vegetative or transforms into a flower primordium. In a number of plants this transformation is affected by length of day.
2. *Initiation.* Number and place of organs is established. Blaauw *et al.* (1932) showed that in the tulip flower temperature affects the number of flower parts initiated.
3. *Determination.* Nature of initiated organ becomes established. Differentiation of tissues starts. Organ attains its essential form. May be influenced by level of nutrition (De Vries 1903).

3 *bis. Dedifferentiation.* Differentiated cells become meristematic again and may give rise to any structure. Occurs in case of regeneration of new organs on old ones. In many instances high auxin concentrations cause dedifferentiation.

B. Physiological stages, easily influenced by external conditions.

4. *Elongation.* Increase of embryonic organ to final size, mainly through cell enlargement.
5. *Maturation.* Final chemical changes in the full grown cells and tissues.

In the described tomatoes all stages of fasciation as summarized by Schoute (1936) were observed: typical fasciation both in vegetative and generative meristems, and radiate and ring meristems in flowers. In addition spiral fasciation was observed in a flower primordium, comparable with biastrepsis in stems. On the other hand no connations in stems were found. The typical fasciation is present in a very modest degree in vegetative stems, and there usually leads to dichotomy. In most cases the foliar spiral has started to show abnormalities some nodes below the dichotomy, and then no conclusion can be reached as to the relation of the direction of the foliar spiral in the two branches to the original direction. In some of these cases the two branches had opposite spirals. But in two stems where dichotomy occurred practically without previous phyllotactical disturbance, both branches followed the original direction of the foliar spiral.

Tricotyledonous plants are interesting in connection with fasciation. We have to assume that such a condition arises through enlargement of the growing point, so that three instead of two cotyledons can be initiated simultaneously in a whorl. This enlarged growing point persists for a shorter or longer period afterward, so that the first leaves also form in a whorl of three. Then either the size of the growing point decreases again to normal and a $\frac{2}{5}$ phyllotaxis appears, or the whorled condition persists until the enlarged growing point splits in two and true dichotomy results. In most other cases (except fig. 15) dichotomy is preceded by an increased number of leaves in the foliar spiral, decreasing the divergence to well below 120°. This also indicates enlargement of the growing point previous to the actual bifurcation.

SUMMARY

The more important abnormalities observed in the development of the tomato plant are as follows:

Anomalous phyllotaxis occurs in 5–20 per cent of the plants just below the first inflorescence. The upper 3–7 leaves are supernumerary and appear more or less whorled. Since all intermediate stages between a normal calyx primordium and a normal leaf complete with axillary bud have been found, it is concluded that these upper whorled leaves are transformed calyx primordia.

Flower primordia develop into normal flowers only after the 14th–17th foliage leaf. Flower primordia initiated before so many leaves are formed remain arrested in early stages of development and differentiation, but enlarge to some extent. In this way models of flower primordia are produced, which clarify a number of problems connected with flower initiation.

The influence of temperature on some of these morphogenetic processes is described.

Various forms of fasciation, especially in flower primordia, are observed and described.

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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 71, NO. 1, PP. 93–98 JANUARY, 1944

PECULIAR FERN PROTHALLIA

W. N. STEIL

INTRODUCTION

In several cultures of gametophytes of a species of *Tectaria*,[1] the spores of which were obtained from the Botanical Garden of Leiden, Holland, April 20, 1935, there appeared a number of peculiar gametophytes of another fern, undoubtedly of a *Dryopteris* species. Young sporophytes produced by the gametophytes of the fern were typically those of *Dryopteris*. In a number of other cultures made later from sowings of spores obtained from the same Botanical Garden, the observations herein described have been confirmed.

The cultural conditions under which the gametophytes were grown have been described by the author (1919).

THE VARIEGATED GAMETOPHYTE

The prothallia were examined from time to time, but showed no peculiarities until they became quite large and heart-shaped, when definite regions of different degrees of intensity of color, varying from green to white, made their appearance. Several well defined regions of this nature are shown in a photomicrograph (fig. 1) of the anterior portion of a prothallium. Just posterior to the apical notch is represented a triangular light green region almost completely surrounded by a nearly albinic one. Other portions of the prothallium are also characterized by nearly albinic cells. When the cells of the regions of the gametophyte, which appeared almost white, were examined under the microscope, it was readily observed that they contained fewer and smaller as well as paler plastids than the ordinary cells of the prothallium. The walls of these cells are also thinner than those of the darker green cells (fig. 1). The outer portions of the lobes of the gametophyte are composed, to a considerable extent, of cells which contain so many ordinary chloroplasts that the cells appear black in the photomicrograph. A variegated secondary gametophyte with several nearly albinic portions is represented by figure 2. A gametophyte originating from one of the lobes of the secondary gametophyte possesses only green cells.

In some of the gametophytes, no such definite regions varying in intensity of color as described above are present. Instead, the chlorophyllose and the nearly albinic regions are composed of smaller or larger groups of cells (figs. 3, 4, 6).

[1] Labeled *Dryopteris trifoliatum*. It has been impossible to obtain fronds of the fern for positive identification.

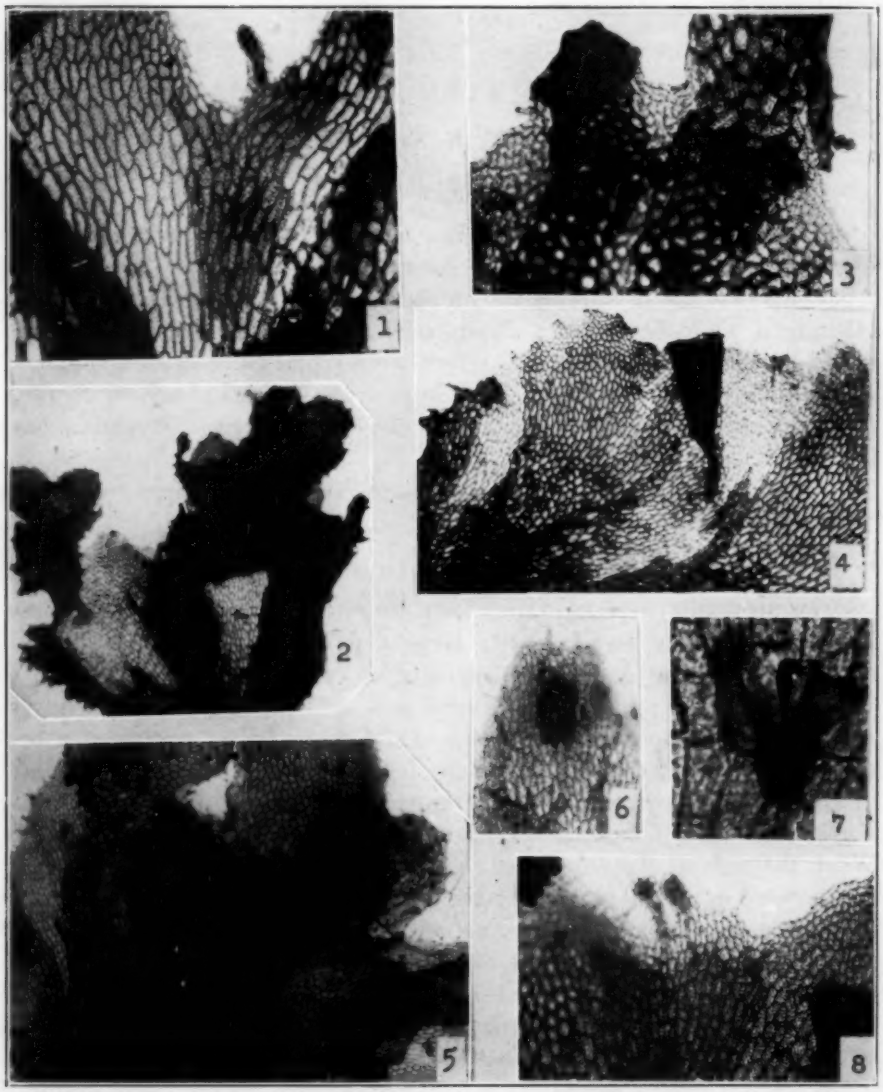

Fig. 1. A variegated gametophyte showing a pale green wedge-shaped portion in the region of the apical notch. This region is almost surrounded by a nearly white portion. The gametophyte also shows a short sporangium-like outgrowth from the apical region. ×35. Fig. 2. A photomicrograph of a secondary gametophyte. Several nearly albinic portions are shown in the figure. ×35. Fig. 3. A photomicrograph of a small portion of a gametophyte showing the nearly white and the dark-green portion. ×40. Fig. 4. A photomicrograph of a small portion of the anterior end of a gametophyte which shows clearly the variegation. ×25. Fig. 5. A photomicrograph of a large gametophyte bearing sex-organs on both surfaces. Numerous archegonial projections and secondary antheridia were also formed on both surfaces. ×20. Fig. 6. A photomicrograph of a portion of a variegated

These regions of the gametophyte just described were generally quite common, especially in the apical portion, and also occasionally in the posterior region of the prothallium.

The majority of the primary and the secondary gametophytes (fig. 2) were characterized by definite regions varying from dark green to nearly white.

The regions of triangular form originate, no doubt, from segments of the apical cell. When the apical cell divides, it loses chloroplasts to its adjacent segments on either side. Hence, further divisions of the segments may result in a nearly white or a pale green region as the apical cell continues to divide. If, at an early stage in divisions of the segments, the chloroplasts continue to multiply, other zones outside of the original triangular region may be produced.

The regions of white or pale green in other portions of the gametophyte cannot be accounted for in the manner described. The formation of lighter and darker regions involve, no doubt, ordinary cells of the gametophyte. Since such cells retain their power to divide for only a short time, the regions of pale green or nearly white are much limited in size. These gametophytes are similar to those first described by Andersson (1923) in *Adiantum cuneatum*, and later in other species of ferns by Andersson-Kottö (1930, 1931) who made a detailed study of such gametophytes in several ferns and showed that the variegation is hereditary.

The peculiar gametophytes described by the author, no doubt, also owe their nature to hereditary factors and not to a virus or to cultural conditions under which the gametophytes were grown.

SEX-ORGANS

The prothallia of the cultures when examined on July 5, 1935, had grown to a large size and bore antheridia and archegonia on both ventral and dorsal sides. Since the gametophytes were grown in Erlenmeyer flasks placed on a glass plate, which admitted light also from below, the illumination of the two surfaces of the gametophyte was nearly equal. Hence, the development of the sex-organs on the two surfaces was due to an environmental condition. In the second set of cultures, made at a later time, the prothallia were illuminated only on the upper side and were then observed to produce sex-organs and rhizoids on only the ventral side.

The cushion of the older prothallia frequently appeared to be of unusual thickness and it produced a large number of "archegonial projections"

gametophyte showing a thickened process produced as an outgrowth of the apical notch. ×25. FIG. 7. A photomicrograph of a portion of a gametophyte with tracheids a short distance back of the apical notch. ×120. FIG. 8. A photomicrograph of a gametophyte with sporangia-like structures produced in the sinus region of the gametophyte. ×25.

Stated magnifications are approximate. The author is indebted to Professor F. A. Bautsch, S.J., for the photomicrographs.

(fig. 5) similar to those described by Heim (1896) in *Doodya caudata*. Secondary prothallia in large numbers were formed from these archegonial projections. The antheridia at an early stage in their development often produced secondary prothallia. Frequently antheridia originated from the lid cell, or a ring cell of the antheridium. Sometimes the single initial cell of an antheridium was observed to form a short filament which produced a prothallium. The formation of secondary antheridia from the lid cell or from one of the ring cells of the antheridium was of common occurrence. The formation of these secondary prothallia and secondary antheridia are similar to those described by Steil (1921) in *Polypodium irioides*.

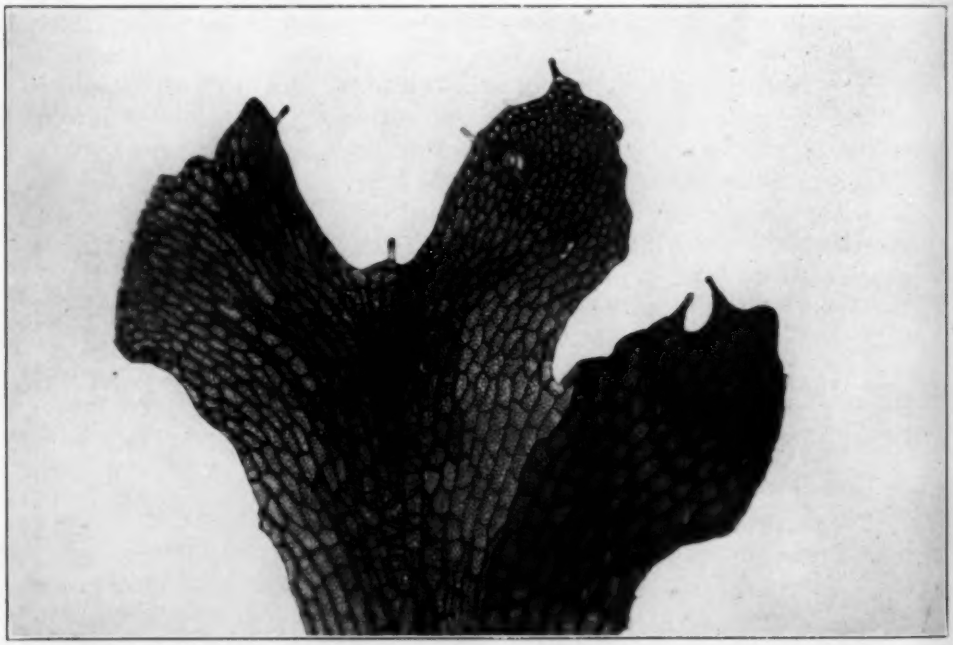

FIG. 9. A photomicrograph of a variegated gametophyte of a *Dryopteris* species. × 40 (approx.).

APOGAMY

Usually a lobe was produced in the sinus region of a gametophyte which had grown to large size (figs. 6, 7). The prothallium occasionally formed a plate of cells or a cylindrical outgrowth from the apical notch similar to that described by Farlow (1874), and Steil (1918, 1919, 1933, 1939) and others in gametophytes of apogamous ferns. Tracheids could be readily observed in the gametophyte, usually a short distance from the apical notch (figs. 7, 8, 9). Frequently outgrowths enlarged at their distal ends

were produced in the apical notch (figs. 1, 8). The enlarged portion, nearly spherical in form, was composed of a definite layer of outer cells and of inner cells of large size and nearly spherical in form. These structures, no doubt, were sporangia, each containing cells resembling spore mother cells. Similar non-functional sporangia originating from the gametophytes of the fern have been described by Lang (1898, 1929). It is obvious that sporangia of this nature, although abortive, are of apogamous origin.

SUMMARY

1. The gametophyte of a fern, undoubtedly of a *Dryopteris* species, is described.

2. A large proportion of the gametophytes were variegated. The trait is of a hereditary nature.

3. The gametophyte, typically heart-shaped, of large size, and bearing numerous hairs, produced antheridia and archegonia in large numbers.

4. The antheridia produced gametophytes and secondary antheridia.

5. The archegonia produced from their neck cells normal gametophytes and antheridia.

6. Archegonia frequently formed "archegonial projections" which finally produced heart-shaped prothallia, resembling in all respects the primary ones.

7. Antheridia, archegonia and rhizoids in one set of cultures were formed on both surfaces of the gametophyte.

8. The gametophyte, so far as could be determined, always produced the embryo apogamously.

9. Sporangia-like structures were occasionally formed from the sinus of the gametophyte.

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Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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